EVOLUTION OF NEOTROPICAL CRICETINE RODENTS (MURIDAE)

WITH SPECIAL REFERENCE TO THE PHYLLOTINE GROUP

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Evolution of Cricetine Rodents

INTRODUCTION[1]

Phyllotines are grazing, or pastoral, cricetines confined to the Neotropical region. They may be as small as house mice or as large as Norway rats. Their ancestors, along with other grazing and aquatic mice, were among the first cricetines to invade South America over the Panamanian land bridge. Today, nearly every important grazing and grazing-browsing range of the Neotropical region from Costa Rica south to the Straits of Magellan, from sea level to more than 5000 meters above, or to the highest points capable of sustaining mammalian life, is occupied by one or more species of

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[1] This paper was submitted for publication in 1956 and was in galley proof when a published revision of the genus *Phyllotis* by Oliver P. Pearson came to hand in December, 1958. Pearson's work includes many advances over our erstwhile knowledge of the systematics and ecology of the species and subspecies included by me in the *Phyllotis darwini* complex. Many of Pearson's contributions are based on a considerable amount of material studied and collected in the field by the author himself. A part of this collection, totaling approximately 400 specimens including the bacula of 113, has since been made available to me by Dr. Seth B. Benson and Dr. Oliver P. Pearson of the Museum of Vertebrate Zoology, University of California. I am particularly grateful to them for their kindness. My study of this material has resulted in an interpretation of the inter-relationship of the members of the *Phyllotis darwini* complex which differs in some ways from Pearson's own.

A number of other important contributions to our knowledge of cricetine morphology and phylogeny also have appeared since 1956. Those pertinent to the present study have been taken into account either in the text or in footnotes. A series of short papers by Vorontsov (1957, 1959a, b, 1960a, b) on the anatomy of soft parts, zoogeography, adaptive radiation and systematics is of particular interest. Unfortunately, Vorontsov's documentation in support of his generalizations and broad conclusions is sparse. The number of specimens dissected is not given and the variety of New World cricetines examined is small. Strangely, Vorontsov gives no indication that he is familiar with the bulk of the recent literature on New World cricetines published in North and South America. Finally, on March 1, 1962, I received the second part of Dr. Angel Cabrera's *Catálogo de los mamíferos de America del Sur*. His classification of the species of *Phyllotis* is that of Pearson. His treatment of the genera *Calomys* and *Eligmodontia* may reflect the content of some of the correspondence between him and me and, possibly, my determinations of a number of cricetines in the collection of the Buenos Aires museum. Other revisions made by Cabrera were not anticipated and corresponding changes in the text could not always be made at this date except by way of footnotes.

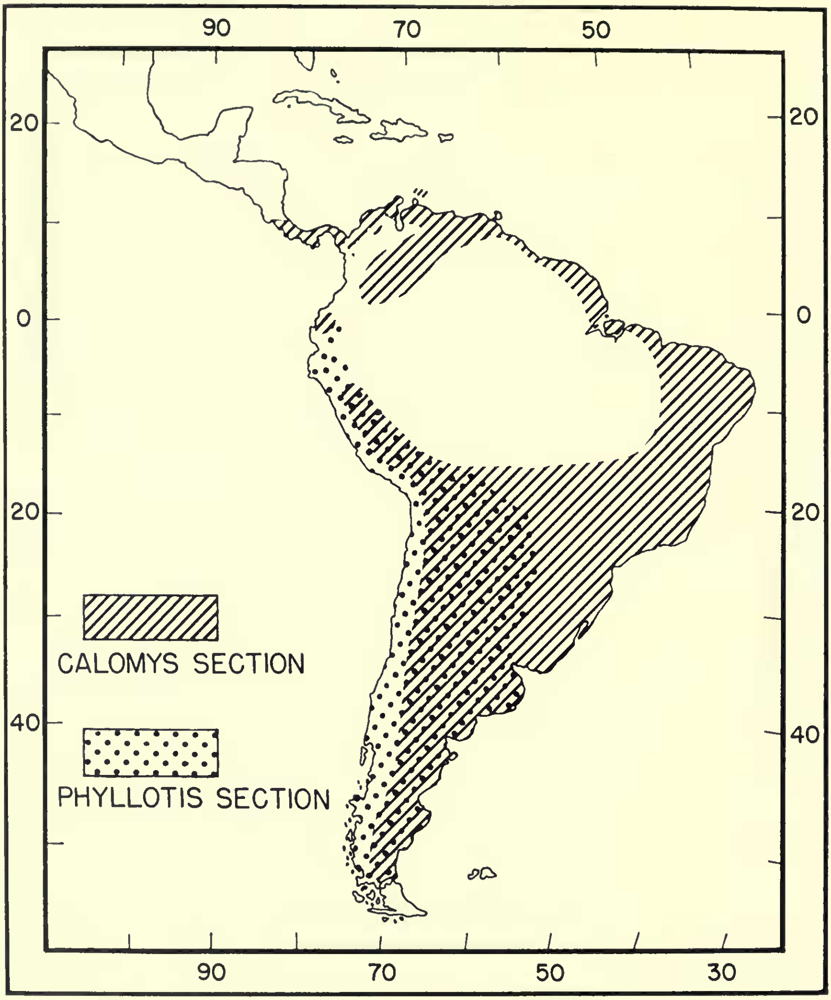

Fig. 1.—Map of South and Central America showing distribution of the phyllotine rodents.

phyllotines (fig. 1). Rapid and pervasive dispersal of the group was promoted by the availability and abundance of natural pastures, by the absence of predatory insectivores, and by the paucity of small, grazing competitors. Man-made pastures and settlements in erstwhile forest country are also being added to the range of phyllotines. *Phyllotis darwini* and *P. micropus* have followed man's clearings along river borders and through forests of Chile and western Argentina. *Zygodontomys* is rapidly becoming the common plague rodent in tropical regions where previously forested areas have been transformed into pastures. Individuals of *Phyllotis darwini*, *P. griseoflavus* and the *Mus*-like *Calomys callosus* and *C. laucha* have invaded man's habitations. These species compete with introduced murines in farms, villages and even in large metropolises. They are among the most successful of indigenous mice and are abundant, often excessively so, throughout their extensive range. One of them, *Calomys laucha*, has been accidentally imported into the tropical coastal areas of northern South America where it is now well established. This is an extension of range far removed from the natural habitat of the species in the temperate zones of southern South America.

MATERIAL

Approximately 2500 specimens of phyllotines were examined. Of these, 2308 are formally listed. The remainder represent *Zygodontomys*, a genus not revised to the subspecies level, though a provisional classification of its nominal subdivisions is given. Characterization of the non-phyllotine *Euneomys*, included in this monograph, is based on 20 specimens.

Present material represents all but 5 of the 132 described forms of phyllotines. These 5, and 16 uncritically listed named forms of *Zygodontomys*, are included in the total of 60 species and subspecies recognized as valid. New names have not been proposed here.

ACKNOWLEDGMENTS AND ABBREVIATIONS

Thanks are expressed to the authorities of the institutions listed below for permission to study and report upon the specimens of phyllotines in their charge. The following abbreviations for the names of the institutions are used in the text and lists of specimens examined.

AMNH = American Museum of Natural History
BM = British Museum (Natural History)
CNHM = Chicago Natural History Museum
LACM = Los Angeles County Museum
RNHL = Rijksmuseum van Natuurlijke Historie, Leiden
MACN = Museo Argentino de Ciencias Naturales, Buenos Aires
MCZ = Museum of Comparative Zoology, Harvard University
MVZ = Museum of Vertebrate Zoology, University of California

A critical reading of a draft of this manuscript by Professor Bryan Patterson is gratefully acknowledged. I am specially thank-

ful to Staff Artists E. John Pfiffner and Marion Pahl and Photographers John Bayalis and Homer V. Holdren for the illustrations.

MEASUREMENTS

All measurements in the tables are given in millimeters. Figures in parentheses are the extremes, the mean precedes the parentheses, and the number of samples measured follows.

Cranial terms and measurements are explained in figures 22-26. Except as noted, external measurements are those of the collectors and are not uniformly comparable. Unless otherwise indicated, measurements of "hind foot, dry," include the longest claw and were taken by the author.

Ordinarily, altitudes and distances are given in the universal metric system. However, measurements recorded in feet and miles on specimen labels and in published descriptions have not been changed in the following lists of localities. Some collectors and authors have perversely converted into the English system altitudes and distances originally or officially recorded in the metric system. To reconvert such measurements here would compound errors of arithmetic and errors of judgment.

ORIGIN, EVOLUTION AND DISPERSAL

The earliest New World cricetines may have appeared during early Oligocene or even late Eocene. They may have originated in Eurasia and ranged into North America, or they may have arisen in North America and extended into the Old World. Whatever the place of origin, modern Old World cricetines are relatively few in kind, specialized in form, and pastoral in habitat. American species, on the other hand, are highly varied and occupy a diversity of pastoral and sylvan niches.

The ancestral form was essentially terrestrial and, judged by present habitats of cricetines with unmodified molars, a forest dweller. Its diet consisted mainly of succulent herbs, fruits, fungi, soft seeds, shoots, exposed roots, insects, and other small invertebrates. The molars were characterized by low crowns, a double row of moderately raised and rounded cusps, and three connecting crests, or lophs. These are the pentalophodont molars described in detail elsewhere (p. 76). They are designed for efficient mastication of food chiefly by crushing and pounding motions of the lower jaws. Other characters of the ancestral species include a *Mus*-like form and size, tail approximately equal to combined head and body length, toes well developed, sole and tail coarsely scutellated, skull delicate and generally smooth, rostrum moderately elongated, hard palate wide, comparatively short and unfurrowed, upper incisors simple, slender and recurved. A juvenal pelage distinguishable from that of the adult by its darker color and finer texture is another character of archaic sylvan cricetines. Although the first cricetines (or nearly related contemporaries) are not known, they may have been very much like modern representatives of *Thomasomys*, or typical *Peromyscus*.

The evolution of cricetines resembles that of horses in several important respects. Both categories began as forest dwellers in early Tertiary and both succeeded in spreading over most of the Holarctic region by late Tertiary. Where rainfall failed and forests were replaced by savannas, progressive forms of early equids and cricetines gradually changed into grazers. The transition from sylvan to pastoral life was made possible by the transformation of crested, low-crowned molars into plane, high-crowned molars capable of withstanding the attrition of hard grasses and associated grit. In cricetines, the higher the molars, the earlier their eruption and function. This correlation corresponds to the presence and use of milk premolars by young ungulates. Shortening of the nestling stage and suppression of the distinctive juvenal pelage in pastoral cricetines are other adaptive characters. These compare with adaptations of colts and other new-born grazing mammals which permit them to fend almost entirely for themselves in competition with adults.[1]

[1] Vorontsov (1960b, p. 155) believes that the transition from sylvan to pastoral habits is also "expressed ecologically in the reduction of the animals' mobility, in the increase of the total volume of food consumed, in the transition from nocturnal to 24-hour activity, in the disappearance of the instinct of food provision. . . . Morphologically, this transition is revealed in the reduction of the organs of sense (smell, sight, taste), in the simplification of the organs of movement, in the reduction of olfactory lobes of the cerebrum and cerebellum . . . and essential transformation in the alimentary system."

There is no evidence that the locomotory organs of New World pastoral cricetines are less versatile than those of their comparably specialized sylvan counterparts. The contrary may even be true in specific cases. All cricetines are nocturnal and some species are also diurnal. Stresses and environmental pressures frequently cause diurnality in otherwise nocturnal species. Undoubtedly, pastoral species, because they are more frequently and easily observed by man, appear to be more commonly diurnal than sylvan species. Vorontsov's statement that pastoral species are losing their instinct for food hoarding must be a mistake of the translator (I have not seen the original paper in Russian, if published). Pastoral species are, of course, more regular and consistent storers than sylvan species. Vorontsov himself (1960a, p. 983), speaking of Palearctic cricetines, emphasizes that the "features of their winter biology (food storage and hibernation) permit the present hamster

New World grazing, or pastoral cricetines emerged in three centers. The first was in the western United States during the Oligocene. *Eumys* Leidy and *Leidymys* Wood are two noteworthy products of the center. The same or similar genera may have migrated into the second center in Middle America when grasslands were established there, not later than early Pliocene. It is more likely, however, that the Middle American forms arose independently from the same generally distributed sylvan stock. No fossil records exist to throw light on this subject. The third center of origin of pastoral cricetines is in South America, beginning in late Pliocene or early Pleistocene. The order of invasion of South America by cricetines was determined by the normal sequence of ecological succession on the Panamanian land bridge. The first cricetine habitats established were pastoral, specifically aquatic and palustrine. Savannas, then forests, each with its fauna, followed. It is significant, then, that the progressive and specialized pastoral, rather than the archaic and sylvan cricetines were the first to enter South America. The highly specialized, aquatic ichthyomyines may have been in the vanguard of the invasion. As forests superseded the grasslands of the Andean and coastal regions of northwestern South America, pastoral cricetines (excepting aquatic forms like *Rheomys* and *Ichthyomys*, whose habitats and modes of life were least affected) were pushed into the savannas of the Guianas and into the punas and pampas of the southern half of the continent.

Pastoral cricetines of the Guianan region (including northeastern Brazil) are the phyllotine *Zygodontomys*, the sigmodonts, *Sigmodon* and *Holochilus*, and the relict akodonts, *Chalcomys*, *Microxus* and the oxymycterine *Podoxomys*. All Patagonian cricetines, except the ubiquitous *Oryzomys* (*Oligoryzomys*) *nigripes* (=*longicaudatus*), are pastoral.

Each modern phyllotine species probably originated somewhere within its present range. The ancestral phyllotine was almost certainly Middle American in origin. Its identity with Pleistocene (and late Pliocene?) fossils of the United States, recorded under such phyllotine names as *Hesperomys* (=*Calomys*) and *Eligmodontia*, cannot

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to survive. . . ." Differences in the sense organs and central nervous system certainly exist between many species of cricetines, but a cleavage in these respects between New World sylvan and pastoral forms has not been shown. Evolution of a two-chambered stomach in Old World pastoral species from a primitive sac-like structure such as occurs in New World sylvan *Nectomys squamipes* was demonstrated by Vorontsov (1957, p. 526). On the other hand, the stomach of Old World pastoral *Calomyscus* and nearly all New World pastoral forms examined by Vorontsov remains single-chambered.

be demonstrated. What appears, nevertheless, is that molars of pastoral cricetines are remarkably similar in all geographic centers of origin, whether New World or Old World.

CLASSIFICATION AND INTERRELATIONSHIP

Cricetines, including phyllotines, are here regarded as a subfamily of Muridae. Differences between the Murinae and Cricetinae are weak and depend almost entirely on whether or not stylar processes on the inner side of the upper molars are hypertrophied into functional cuspules. The addition of one or more such cuspules results in the complicated triserial tubercular pattern characteristic of Murinae as distinguished from the primitive biserial pattern retained in the Cricetinae. Actually, the difference is no more significant than the dental ones separating such cricetines as *Oryzomys*, *Peromyscus* (s.s.), *Thomasomys* and *Aporodon*, all with a functional mesoloph fused with the mesostyle, from other cricetines such as *Neotoma*, *Sigmodon*, *Hypsimys*, *Ichthyomys*, etc., without mesoloph and mesostyle. Indeed, the Murinae and all other supergeneric groups of living Muridae, save some Malagasy species, diverged from a cricetine stock in which the mesoloph was being eliminated. Notwithstanding gross differences between the extremes of the groups concerned, the record of change from species to species, genus to genus and subfamily to subfamily, is still preserved in Recent forms.

Perhaps more basic than the structure of the molars as a criterion in the classification of myomorph rodents is the design of the baculum and glans penis. Two basic types of penes in the Cricetinae, and possibly in the Muridae as a whole, have been demonstrated by Hooper (1959, 1960) and Burt (1960). The *simple* type of penis contains a baculum made up of a bony shaft and a single cartilaginous segment at the tip. The baculum of the *complex* type is composed of a bony shaft with three osseous, cartilaginous or soft tissue fingerlike processes attached to the tip (fig. 5). According to Hooper (1960, p. 17) the complex or quadripartite baculum with its correspondingly complex glans penis "is the common and geographically widespread one. It is predominant in cricetids (sensu Simpson, 1945) in both the Old and New Worlds, and likely it is typical of murids. It occurs in *Mus*, *Rattus*, *Apodemus*, *Micromys*, *Acomys*, *Arvicanthis*, *Nesokia*, *Meriones*, *Rhambomys*, *Cricetus*, *Cricetulus*, *Mesocricetus*, most if not all microtines, and most if not all South American cricetines [except *Aporodon* and *Tylomys*].

"While the complex plan is widespread, both taxonomically and geographically, the simple type is restricted to a few North American kinds. Of the 50 or more genera studied to date, the following twelve are characterized by simple glandes and bacula; *Peromyscus, Reithrodontomys* [including *Aporodon*], *Neotomodon, Ochrotomys, Onychomys, Baiomys, Scotinomys, Nelsonia, Neotoma, Xenomys, Ototylomys* and *Tylomys*." This assemblage of genera, concludes Hooper (1960, p. 19), "has the aspect of a distinct natural unit, of subfamily or family rank, which like the Heteromyidae and Geomyidae, is endemic to the New World. The possibility that it is a natural group now requires intensive investigation, utilizing all pertinent anatomical data."

That these twelve or thirteen genera comprise a natural group distinct from other cricetines seems to be confirmed by their cranial, dental and external characters. The differences between the genera *inter se* are typical of radiating forms and each genus could have diverged from a common *Peromyscus*-like ancestor. As a result of convergence, sylvan and pastoral peromyscines strongly resemble their ecological equivalents among South American cricetines. The similarities between sylvan *Peromyscus* of the simple penis group and sylvan *Thomasomys* of the complex penis group, however, may be more than superficial. These genera occupy a position very near the point of dichotomy between their respective phyletic lines and their kinship is correspondingly close. On the other hand, resemblances between pastoral *Baiomys* with simple penis and pastoral *Calomys* with complex penis are superficial and clearly the result of convergence. The trenchant differences between these two genera are discussed elsewhere (p. 126).

The systematic value of the structure of the cricetine penis cannot yet be fully appreciated or properly interpreted. The penes of the vast majority of the species and genera remain to be studied and critically compared and there is no fossil record. What is known of the differences between the two types of bacula and their glandes is not imposing. Conceivably, if not predictably, the two types may prove to be fully intergrading. No other basic anatomical character absolutely distinguishes any one supergeneric group of murids from another. Nevertheless, such characters are important and those of the penis or its parts may be transcendental.

The taxonomic significance of the structure of the cricetine alimentary tract, particularly of the stomach, has been examined by Vorontsov (1957, p. 526). This investigator demonstrated the presence of a two-chambered stomach in representatives of all Palearctic

Cricetinae except *Calomyscus*. Among New World cricetines he found a simple sac-like stomach in *Nectomys squamipes, Sigmodon hispidus, Reithrodontomys megalotis* and, from published data, in *Peromyscus leucopus, Neotoma floridana* and *Oxymycterus rufus*. In addition, Vorontsov noted the tendency for the formation of a three-chambered stomach in *Haplomylomys californicus* and that the single-chambered stomach of *Nectomys squamipes* most nearly resembled the postulated primitive cricetine condition (see also footnote, p. 18).

From the foregoing, it is presumed that microtines and South American cricetines, both with complex glans penis, and peromyscines, with simple glans penis, arose independently from a common cricetine ancestor. The ancestral type may have been very much like modern *Thomasomys* with the complex glans penis and a single-chambered stomach. Presumably, most New World cricetines, whether sylvan or pastoral, retain the simple stomach. Old World cricetines and murines may have diverged from a common stock which, in turn, was itself an independent offshoot from the original thomasomyine stock. Only *Calomyscus* among Old World murids has kept the structurally simple stomach.

Widest cleavage among South American cricetines exists between forest, or *sylvan*, forms and their progressive *pastoral* relatives (fig. 2). Morphological differences between the two divisions are of the same order, though weighed on finer scales, as those distinguishing primitive browsing horses from their grazing descendants. In the case of murids, however, it is common for certain primitive ancestral stocks to exist contemporaneously with their modern specialized descendants and connecting relatives.

The older sylvan division includes thomasomyines (*Nyctomys, Otonyctomys, Phaenomys, Rhipidomys, Thomasomys* [*Wilfredomys* Avila Pires, a synonym]) and oryzomyines (*Oryzomys* [sensu lato], *Nesoryzomys, Neacomys, Scolomys, Megalomys*). In these, each tooth of the molar series is pentalophodont, i.e., with mesoloph (-id) present and fused with mesostyl(id) (figs. 4, A; 10, A; 11, A, B; 13). Sylvan cricetines are primarily inhabitants of broad-leaf forests (*selva*). The terrestrial species habitually nest on the ground or in dry burrows. They may forage in trees, streams and lakes as well as on the forest floor. Arboreal cricetines nest, feed and breed in trees but sometimes descend for food and water. Semi-aquatic forms nest on the banks of streams or lakes. There are no fossorial sylvan cricetines.

The pastoral division includes akodonts, phyllotines, sigmodonts, ichthyomyines, oxymycterines and every other South American crice-

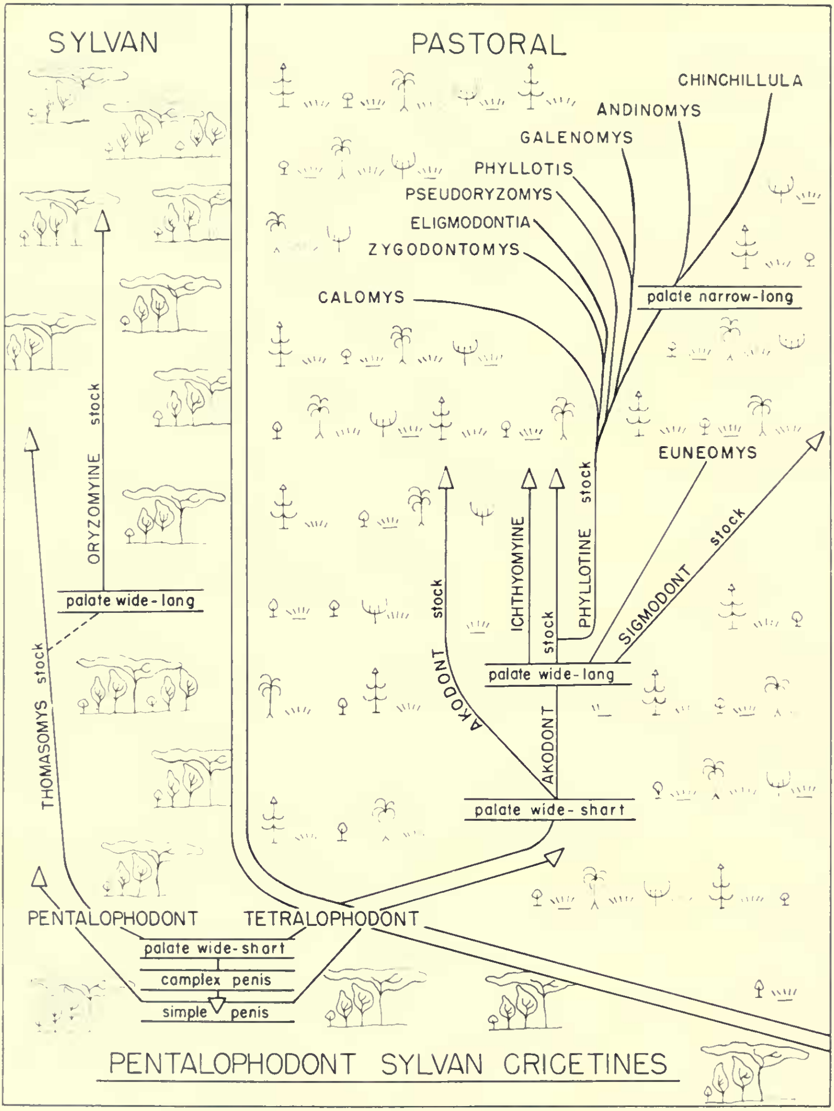
SYLVAN
PASTORAL
CHINCHILLULA
ANDINOMYS
GALENOMYS
PHYLLOTIS
PSEUDORYZOMYS
ELIGMODONTIA
ZYGODONTOMYS
CALOMYS
palate narrow-long
EUNEOMYS
ORYZOMYINE stock
palate wide-long
THOMASOMYS stock
AKODONT stock
ICHTHYOMYINE stock
PHYLLOTINE stock
SIGMODONT stock
palate wide-long
AKODONT
palate wide-short
PENTALOPHODONT
TETRALOPHODONT
palate wide-short
complex penis
simple penis
PENTALOPHODONT SYLVAN CRICETINES

FIG. 2.—Interrelationship of the phyllotine genera and their morphological and ecological relationship to certain other South American cricetines. The progressive pastoral forms with tetralophodont molars evolved from sylvan pentalophodont stock. Cricetines with a simple type of penis probably evolved from a sylvan pentalophodont stock with the complex type of penis.

tine not named above as a member of the sylvan division. Their molars are simplified, i.e., with mesoloph absent, or, if present, reduced and never fused with the mesostyle. The mesolophid is universally absent or obsolete. The molar pattern is tetralophodont, or may be reduced to trilophodont, bilophodont or cylindrodont (figs. 4, B-D; 10, B–F; 11, C, D). Pastoral cricetines inhabit pampas, punas, llanos, savannas, tundras, scrublands, rock lands, deserts and other types of grazing and grazing-browsing habitats. They also occur in thick second-growth woodlots during early seral stages, and in narrow leaf, or coniferous forests. Most pastoral species are terrestrial and nest on the ground or in burrows. Semiaquatic forms shelter along the banks of watercourses. A few species are fossorial and certain scansorial species have acquired arboreal nesting habits in scrub country subjected to periodic inundations and destruction of ground cover usually by burning.

A number of sylvan cricetines may be excurrent elements in pastoral regions, especially along streams and gallery forests. Conversely, pastoral species may be incurrent in forests where waterways, grassy banks or deforestation provides avenues of ingress.

Sylvan and pastoral members of the peromyscine group differ in the same way as the corresponding divisions of the South American cricetine group. In some cases, however, species or even subspecies notably of the genus *Peromyscus* (cf. Hooper, 1957) appear to be intermediate between pastoral and sylvan divisions in habitat and molar design. They are best included in the pastoral division toward which they are evolving rather than with the sylvan group whence they departed. Certain other species, such as the woodrat (*Neotoma floridana*), with dentition highly specialized for pastoral life, have acquired sylvan habits in parts of their range.

All microtines and Old World cricetines are pastoral. Their habitats and habits are similar to those of South American pastoral cricetines and their dental evolution has followed parallel lines.

Phyllotines belong to the pastoral division of South American cricetines. They may be recognized chiefly by their generally *Mus*- or vole-like appearance, light or moderately heavy skull without salient modifications, long *Oryzomys*-like palate with conspicuous posterolateral pits, long slender incisive foramina, and tetralophodont molars, i.e., molars with mesoloph (-id) obsolete or absent (fig. 4, B). Phyllotines probably evolved from the same line that gave rise to akodont rodents. The sigmodonts (*Sigmodon*, *Reithrodon*, *Neotomys*, *Holochilus*) are more specialized but appear to be progressive offshoots from the main phyllotine line. The Neotropical fish eaters typified by *Ichthyomys* and *Rheomys,* also with basic tetralophodont molars, are highly specialized derivatives of pastoral forms. The insectivore-like oxymycterines represent still another radiation of basic pastoral stock (fig. 2).

Phyllotines are separable into two sections. The more primitive *Calomys* section includes the buno-brachyodont *Calomys, Eligmodontia* and *Zygodontomys.* The *Phyllotis* section, with high-crowned, terraced or planed molars (fig. 14), consists of *Phyllotis, Pseudoryzomys, Galenomys, Andinomys* and *Chinchillula.* The *Mus*-like *Calomys sorellus* and *C. laucha* are the most generalized and smallest members of the phyllotine group. The microtine and hamster-like *Andinomys* and *Chinchillula,* respectively, are the most specialized and largest. External and cranial differences between the extremes are hardly more trenchant than those separating species and subgenera. On the other hand, dental differences between *Calomys* and either *Andinomys* or *Chinchillula* are of the same order as those distinguishing a browsing buno-brachyodont ungulate of the Oligocene from its modern grazing platy-hypsodont descendant. In phyllotines, however, evolution in dental topography from low crown to high crown, from crested to plane, from tetralophodont to bilophodont (fig. 10), can be traced as a gradual transition through living species.

Besides the generalized tetralophodont dental pattern, the species of *Calomys* exhibit in their crania the two basic supraorbital types (fig. 23) found in cricetines. One is with parallel- or concave-sided supraorbital region, the other with divergent-sided supraorbital region. All generalized external characters of phyllotines are found in *Calomys.* It may be assumed, therefore, that the pre-phyllotine ancestor differed little in external and cranial characters from such forms as *Calomys sorellus* and *C. laucha.* The ancestral molars, however, must have been marked by the presence of a well-developed mesoloph. This is requisite for derivation of phyllotines from the basic pentalophodont cricetine stock.

The remarkable resemblance between *Calomys* and the distantly related tetralophodont *Baiomys* of North America is principally superficial and appears to be the result of convergence (cf. p. 126). Certain gross resemblances between phyllotines and South African *Mystromys* (cf. p. 221) are obviously the result of parallel development of widely separated lines of murids.

The most specialized phyllotines grade into the sigmodont group (for characterization see Hershkovitz, 1955, p. 640).[1] Molars of sigmodonts are, in general, more advanced, with the enamel folds more compressed and tending toward lamination. The palate and the pterygoid region are more complicated, the zygomatic plate extremely developed. Externally, sigmodonts, which have developed such well-defined vole-like, aquatic, and leporine types, may be nearing the end of their adaptive radiation.

External, cranial and dental criteria for classification of the cricetines mentioned above are discussed under separate headings below.

ADAPTIVE RADIATION

The repeated establishment of meadows, prairies, tundras and coniferous forests in the wake of the several glacial retreats in the northern hemisphere provided the stages for explosive developments of pastoral murids from sylvan stock. With the close of the last glacial period, pastoral forms diversified into many types, each adapted to a special niche.

Notwithstanding differences in general environment, diet and masticatory systems, adaptive radiation in pastoral species was remarkably similar to that of sylvan species where newly invaded habitats resembled sylvan habitats. In the case of Neotropical cricetines, the semiaquatic, pastoral marsh rat, *Holochilus*, is almost indistinguishable in external and cranial characters from its sylvan counterpart, the oryzomyine rat, *Nectomys squamipes*. Pastoral but semiarboreal *Phyllotis griseoflavus* mimics its sylvan opposite numbers among scansorial or more or less arboreal species of *Thomasomys*, *Peromyscus* (*Megadontomys*) and *Oryzomys* (*Oecomys*) *concolor*. Not only do these species agree in body size, proportionate tail length and limb modifications; they have also developed a broad, divergent-sided supraorbital region. Truly arboreal pastoral forms comparable to sylvan *Rhipidomys*, *Nyctomys* and *Tylomys* do not exist. Among hystricomorph rodents, however, the grazing-browsing species of *Dactylomyinae* nest and feed in the evergreen pastures of bamboo grove canopies; presumably, the ancestral dactylomyines left the ground when their terrestrial habitat was subjected to protracted floodings or was choked by superseding forests. The most common pastoral cricetine types are vole-like phyllotines, akodonts, etc. The sylvan counterpart is *Oryzomys caliginosus*. Perhaps because of the abundance of moist, dark cover on forest floors or because of periodic flooding in many parts of their range, sylvan cricetines have not become specialized for subterranean life. At best they are weak burrowers. In contrast, the pastoral akodont *Notiomys*, with stout limbs, long claws, minute ears, and thick coat, is well adapted for a burrowing life. Pastoral *Oxymycterus*, *Thaptomys*, and *Bolomys* are subfossorial, and *Blarinomys* is the extreme example of talpine form and habits among cricetines.

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[1] In the description of the cranial characters of the sigmodont rodents, the anterior border of the zygomatic plate is said to be "convex" (loc. cit., last line). The term should read "concave." See plate 29 of the cited work.

The majority of phyllotines are generalized pastoral types. None is fossorial, although most phyllotines do occupy, whether for refuge or nesting, burrows made by other animals. Only the monotypic phyllotine *Pseudoryzomys* is sufficiently modified for aquatic life for comparison with such semiaquatic cricetines as *Oryzomys palustris* *Zygodontomys*, notably in its fan-shaped hind foot, also bears some resemblance to large palustrine types of oryzomyines. *Zygodontomys*, however, is basically vole-like and apt to be confused with the similarly vole-like *Sigmodon*, with which it shares habitats where the ranges of the two overlap. Indeed, the microtine or hamster-like form has been the principal evolutionary line of adaptation followed by phyllotines. *Phyllotis sublimis*, *P. boliviensis*, *Galenomys garleppi* and tiny *Calomys lepidus*, all of the Andean highlands, are short-tailed vole-like inhabitants of grass and rock communities. The last species superficially resembles species of Old World *Cricetulus*. The most remarkable hamster-like phyllotine is the large, heavy-bodied and variegated *Chinchillula sahamae*, of the same habitat.

Eligmodontia typus has radiated in a direction unique among phyllotines and New World cricetines in general. It is remarkably gerbil-like in color, size, shape of body, specialization of hind legs and feet, and choice of habitat. The Piura desert mouse, *Phyllotis gerbillus*, is similar in size, color and habitat but its limbs are not gerbil-like.

A third type of adaptive radiation among phyllotines is the semiarboreal. *Phyllotis griseoflavus* has already been mentioned as the example. This species nests on and above the ground but is primarily a ground feeder. Ability to climb is in itself a generalized phyllotine character.

The vaulted skull and proodont upper and procumbent lower incisors found in the vole-like phyllotine *Galenomys garleppi* of the high Andes are characters pointing to leporine habits. Similar characters exist in the Arctic hare, *Lepus arcticus.* The habitats of both animals are also similar.

JUVENAL CHARACTERS AND DEVELOPMENT

In grassland cricetines the first post-natal pelage is essentially as in adults, though it is usually thinner, paler, and more grizzled on the upper parts and sides of the head and body. Molt from juvenal pelage to typically adult pelage is generally unmarked by lines of transition and is completed during an early stage of development, possibly at weaning.

Growth of tail, hind foot, and ear in young individuals is faster than growth of head and trunk. After sexual maturity, the extremities have attained almost maximum size and their rate of growth declines sharply. Growth of head and body, on the other hand, continues apace throughout life. Measurements reveal that in any one population extremities of juvenals and subadults are proportionately larger than in adults of the same population, and that differences in skull lengths between young and extremely old adults are greater than between young adults and weaned juvenals.

Breeding begins at a growth stage when cranial characters would be subadult or even juvenal. Sexual maturity precedes anatomical maturity in all mammals but pastoral mice are particularly precocious breeders.

The braincase is proportionately larger, the supraorbital region broader in juvenals. In some phyllotines, notably *Phyllotis griseoflavus, Calomys callosus* and *Zygodontomys,* the broad juvenal supraorbitals have been retained in the adult and have developed beaded projecting ledges.

The young of most phyllotines acquire a fully erupted and functional set of molars while still suckling. This phenomenon provides maximum molar surface in response to an early need for grinding siliceous grasses and other harsh, highly cellulose plants. The newly erupted hypsodont or subhypsodont molar is pyramidal in form. As a consequence the grinding surface of the tooth increases with wear concurrently with the growth of the mouse and its need for more food. Some dental elements, such as the mesoloph, normally absent in the adult molars of phyllotines, may be present, though weakly developed, in the newly erupted third molar. Conversely, dental characters of a caenogenetic nature may also appear in the unworn or unerupted third upper molar. Some such characters are ephemeral and of no significance beyond the brief span of their existence. Others may have some selective value and may develop into important factors in the economy of the adult.

The fully adult pelage and dentition acquired at an early age by juvenals of most phyllotines contrast sharply with the distinctively dark pelage and retarded last molar in juvenals of forest-dwelling cricetines with the primitive, or pentalophodont, type of molars.

REPRODUCTION

In Neotropical regions with well-defined seasonal fluctuations in temperature, breeding activity among cricetines is greatest in summer (December–March) and least in winter (June–September). Breeding becomes more nearly uniform throughout the year in latitudes nearer the equator. Here, too, some periodicity may be maintained locally, but mating does not take place at the same time in all localities. In effect, reproduction, like molt, is uninterrupted in species occupying geographic ranges which embrace highly diversified but locally constant climates.

The condition of the mammae in skins of specimens examined indicates that from two to at least four litters are produced annually by the adult female of all species of *Phyllotis*. According to collectors' data, a litter contains from three to ten young. Litter sizes and reproductive rates in phyllotines are comparable to those of cricetines of the Temperate Zone of North America.

Data on sexual behavior, compiled from the literature, are given in the accounts of individual species.

POCKET POPULATIONS

Small mammals of a sedentary nature, such as most phyllotines, are often distributed in *pockets*, when their population is at mean or low levels. A pocket is a small isolated ecological community inhabited by an inbreeding population, or colony, of animals. The pocket ordinarily contains all elements needed for maintaining its resident population and is usually sufficiently diversified ecologically to include a number of niches. A desert oasis and an alpine meadow are examples of pockets in so far as concerns the small mammals restricted to each. A bamboo grove or a wood-lot surrounded by grassland or swamp or, conversely, a pasture or swamp surrounded by forest, each with its special complement of resident animals, are also examples of pockets.

The actual size of a pocket is related to the size and mobility of its residents. A pocket in terms of a cricetine rodent is not a pocket in terms of a large ungulate or carnivore. On the other hand, microscopic organisms infesting a pocket of mice are also residents of precisely the same pocket. Here the *focus* of infection and the pocket are identical and the parasites are subject to the same dynamics of the pocket as their hosts.

The size of the population depends on the carrying capacity of the pocket. Usually, fluctuations in population are directly related to fluctuations in food supply. Rate of reproduction, predation, disease, seasonal changes in climate and terrain are controlling factors. At times of extraordinary abundance of food the population of a pocket may grow to exceed by several times the ordinary carrying capacity of the range. With swift termination of the special food supply most of the population erupts into the inhospitable countryside in search of nourishment. Nearly all migrants die within days (see *ratadas*, p. 42). A few return to their original pocket. Others may breach barriers and find other pockets where they may either be absorbed by established colonies, if any, or start new colonies.

The stability of a pocket population is relative. Its isolation may break down during population explosions or other crises. Floods not only have the power to destroy but may also be the agents for transporting individuals from one pocket to another or for seeding new pockets. Predators or disease may wipe out the population of a pocket and fires may destroy the pocket as well as its population. Pockets themselves may be early seral stages and each major change in succession often involves the displacement or replacement of the earlier pocket population. Cultivation of land by man regularly results in the establishment of new pockets and the destruction or modification of old ones. As pockets expand their populations expand. Two or more pockets which grow and join to form one large subclimax or climax merge their populations into one race. Secondary fragmentation of the climax redivides the racial population into relict pocket populations.

The pocket population is the basic stock for experiments in evolution and the pocket is the primary testing laboratory. The population of a relict pocket is, perhaps, the most stable for experimental purposes and the relict pocket itself provides the most uniform selective pressures for testing new characters or new combinations of characters. When the population is low and the reproductive rate high, the establishment of a trait throughout the pocket population can be rapid. When the population is at an eruptive peak, diffusion of the trait throughout the range of the race or species becomes possible.

The rate of evolution is measured in generations, not calendar years. Pocket populations of small rodents such as phyllotines breed early, usually within one month of birth, and several times each year. The average life span of the individual, however, is less than 6 months. This combination of fecundity and longevity results in rapid population turnovers with a minimum of ancestral genetic drag.

The diagnostic characters of old established neighboring pocket populations may be concordant where ecological conditions are similar, discordant where they are notably different, or clinal where they are varied or intermediate. Differences between allochronic but sympatric populations may be of the same order as differences between synchronic but allopatric populations.

Montane mammalian populations that occupy pockets at the highest altitudinal levels may be called *pinnacle* populations. They are derived from and may retain their connection with the mass of the species population at lower levels. Pinnacle populations of the same mountain system generally develop along parallel or convergent lines but the relationship between them is through the parental stock at lower levels. Where the parental stock has disappeared each pinnacle population becomes a relict evolving along independent lines.

Oasis populations are usually of waif or accidental origin and their superficial characters are generally concordant, their underlying ones usually discordant.

Peripheral pocket populations inhabit the outer borders of the range of the species or subspecies. The diagnostic characters of these populations are apt to be clinal, with each population, in the case of subspecies, interbreeding almost or quite continuously with the neighboring populations of the same or related subspecies.

A species or subspecies generally includes a number of discordant as well as concordant and clinal pocket populations. There are, nevertheless, valid subspecies and even species (cf. *Phyllotis gerbillus*) with their respective geographic ranges restricted to a single pocket.

Basic data for these generalizations on pocket populations are contained in the following accounts of variation between the subspecies of *Phyllotis darwini*, *P. osilae* and others. The habitats of local populations of *Phyllotis* described by Pearson (particularly in his section on sympatry (1958, pp. 397–405) are, in many instances, examples of pockets.

SYMPATRY AND ALLOPATRY

The practical concept of *sympatric* is taxonomic, not biogeographic. The word, however, can refer to any and all organisms occupying a common geographic area. In order to conserve and emphasize the taxonomic sense of sympatric, a restricted form of the term must be used for representatives of sibling species or different subspecies of the same species whose trails cross during the course of their ordinary movements. A more precise term for this form of sympatric relationship is *synecetic*, proposed by Harper, *et al.* (1961, p. 211). Thus, all synecetic representatives of species or subspecies are sympatric but all sympatric representatives of species or subspecies are not synecetic. Two mammalian subspecies with ranges which interdigitate but do not overlap may be regarded as sympatric but cannot be classified as synecetic. The geographic ranges of fossorial, terrestrial, aquatic and arboreal species of mammals may all overlap—actually they would form a mosaic—but if the animals themselves do not ordinarily cross trails they are not synecetic.

Sympatry, when it occurs, follows divergence of the species or subspecies in geographic isolation. Sympatry may endure for the life of all but one of the coexisting taxons, or it may be cyclical or ephemeral. The spatial ebb and flow of otherwise geographically contiguous or narrowly separated taxons may result in periodic or rare overlappings in range. Migratory species coexisting transitorily with closely related forms are not true sympatriants. A misleading simulation of sympatry may result from the mingling, during an eruption, of two or more well-defined and erstwhile geographically isolated pocket populations.

Sympatric taxons may or may not be reproductively isolated but synecetic taxons are necessarily so. Sympatry, or syneceticity between two or more taxons, is generally regarded as prima facie evidence for their specific separation. There are, however, notable exceptions among mammals, including the rodents under consideration.

Allopatric, the antonym of sympatric, could be correspondingly restricted to geographically contiguous sibling (cognate) species or subspecies. Use of the term for widely separated taxons of any grade dilutes or nullifies its special taxonomic implications.

The intimately related and similar-appearing members of the *Phyllotis darwini* complex offer prime examples of the significance of sympatry and allopatry in taxonomy. All other phyllotines can be classified on the basis of morphology alone.

The northernmost member of the *Phyllotis darwini* group is *Phyllotis haggardi* of the Ecuadorian Andes. It is treated as a full species on the basis of seemingly trivial yet consistent characters which distinguish it from its nearest geographic ally, *Phyllotis andium.* Present data indicate that *haggardi* and *andium* are completely allopatric (fig. 72), but the nearer they are geographically the more similar they appear to be. Whether the cline is a product of convergence or of intergradation is a question that cannot be answered conclusively without the test of sympatry.

In contrast with the above, specific separation of *Phyllotis andium* from *P. darwini* depends entirely on evidence of sympatry. The former is recorded as coexisting in central Peru with three subspecies of the latter. The differences between *P. andium* and sympatric populations of *P. darwini limatus,* and sympatric and at least one synecetic population of *P. d. posticalis* are not impressive. They may be greater than between some allopatric populations of the same taxons including *P. andium* and less than others including *P. andium.* On the other hand, *P. andium* differs grossly from *P. darwini definitus* with which it coexists in the only locality where the latter is known to occur. Whatever the nature of the differences, where *andium* and *darwini* are sympatric they do not intergrade and where they are allopatric they cannot interbreed.

Two subspecies of the same species, *P. darwini rupestris* and *P. d. magister,* coexist in southwestern Peru without intergradation (fig. 73). Unlike the preceding example, where these races are allopatric they can and do intergrade through an intermediate subspecies. The larger race, *Phyllotis darwini magister,* is a poorly defined, questionably separable western Andean extension of *P. darwini posticalis. P. d. rupestris* also seems to stem from *posticalis* stock but it has spread southward along the eastern slope of the mountains and has become significantly smaller and paler. Where *rupestris* meets *magister,* differentiation of the former already has reached the point of reproductive isolation from the latter. Inasmuch as both *rupestris* and *magister* grade into *posticalis,* all are regarded as conspecific.

On the opposite side of the Andes in southern Bolivia and northern Argentina, *Phyllotis darwini rupestris* and *P. d. caprinus* are fully intergrading, though their ranges may overlap at some points. The available evidence, meager and unverified as it is, indicates that the two races are not synecetic (figs. 74, 77).

The most interesting and perplexing case of sympatry among phyllotines is that between *Phyllotis darwini* and *P. osilae*. The range of *osilae* extends as a narrow band along the eastern Andes from central Cusco, Peru, in the north to southern Catamarca, Argentina, in the south (fig. 74). Representatives of *osilae* and *darwini* are recorded as sympatric in 25 localities distributed over the entire length of this range. Two subspecies of *P. osilae* and four of *P. darwini* are involved. Whether or not the two species are actually synecetic in any one locality is moot. Pearson (1958, p. 399) believes that "sympatry of these morphologically similar forms is based upon different habitat preferences."[1] If this is true, the case for regarding *osilae* and *darwini* as distinct species rather than sympatric subspecies is considerably weakened.

The greatest number of sympatric series are concentrated in the Lake Titicaca drainage basin in Puno, Peru. They represent subspecies *Phyllotis osilae osilae* and *P. darwini rupestris*. The number of specimens in the sympatric pairs ranges from one *osilae* and two *rupestris* from Puno, Puno, to eighteen *osilae* and three *rupestris* from Pairumani. The best numerical representation of the two species is the series from Chucuito, which consists of five *osilae* and eight *rupestris*. In no case are the sympatric series large enough to use for calculating the full range of their respective variation. The differences between the species are subtle, and the larger the sympatric series of *osilae* and *rupestris* the fewer and narrower the differences become. In any case, sympatric populations of *osilae* and *rupestris* are more nearly alike than allopatric members of the same races.

Differences between *P. osilae osilae* and *P. darwini posticalis* recorded from three sympatric localities in Cusco, Peru, are fine enough to be overlooked or dismissed as insignificant by the unwary taxonomist. Differences between allopatric populations of these subspecies are of the same order or greater, never less.

P. osilae phaeus is easily distinguished from a peripheral series of *P. darwini posticalis* and the differences between allopatric populations may be greater or less.

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[1] This statement appears to be based on impressions of random trapping results rather than on a scientifically conducted census. Pearson does not relate his catch to the number of trap nights or supply information regarding his trapping methods. The reader is left to believe that other conclusions might be reached by other collecting methods or by other collectors. Judged by data on the labels of his specimens, Pearson's trapping consisted of one or two night stands in each of the vast majority of localities worked. The trapping sites were generally along highways or railways in areas with ecologies repeatedly disturbed and constantly controlled by man during one or two millenniums.

The third concentration of sympatric localities is in central Bolivia, where the range of the localized *Phyllotis darwini wolffsohni* sprawls over a section of the range of *P. o. osilae.* The sympatric populations of the two forms are similar superficially but differ in size and in cranial and dental characters. The differences between the two species here are greater than elsewhere irrespective of the races compared or their geographic relationship. Nevertheless, the tendency toward convergence in sympatry is so strong among phyllotines that *P. darwini wolffsohni* more nearly resembles sympatric populations of the species *P. osilae* than it does the nearest geographic representatives of the subspecies *Phyllotis darwini rupestris* with which it intergrades through *P. d. caprinus.*

Not one of the characters that serve to separate sympatric representatives of *osilae* from *darwini* is valid for distinguishing all *osilae* from all *darwini*. The differences between sympatric populations are of the same order as differences between pocket populations and subspecies of either species. There is no evidence of intergradation between *osilae* and *darwini* where they are sympatric, and there is no evidence that a population of one species of a sympatric pair intergrades with an allopatric (i.e., contiguous) population of the other species (cf. Tables 30–49).

Where sympatric *osilae* and *darwini* are most nearly alike, their resemblance suggests either a recent and comparatively slight divergence from a common ancestor or a convergence in sympatry after initial differentiation in geographic isolation. Absence of intergrades or hybrids points to the latter explanation as more plausible if not most probable.

Representatives of the two species that differ most in sympatry occur at the far extremes of their respective geographic ranges. Their greater divergence involved movements over greater distances through more diversified environments during longer periods of time. Nevertheless, where they meet, the species tend to converge in superficial characters at least.

All the foregoing runs counter to *character displacement* defined by Brown and Wilson (1956, p. 63) as "the situation in which, when two species of animals overlap geographically the differences between them are accentuated in the zone of sympatry and weakened or lost entirely in the parts of their ranges outside this zone. The characters involved in this dual divergence-convergence pattern may be morphological, ecological, behavioral, or physiological. Character displacement probably results most commonly from the first post-isolation contact of two newly evolved cognate species. Upon meeting, the two populations interact through genetic reinforcement of species barriers and/or ecological displacement in such a way as to diverge farther from one another where they occur together. Examples of the phenomenon, both verified and probable, are cited for diverse animal groups [none mammalian] illustrating the various aspects that may be assumed by the pattern."

Divergence in allopatry, i.e., in different but contiguous ecologies, and convergence in sympatry, i.e., in the same broad ecology, are an evolutionary pattern quite the reverse of "character displacement." This pattern is not peculiar to members of the *Phyllotis darwini* complex. It is common among closely related mammals of all orders. As a rule, convergent characters in sympatry are superficial, usually adaptive, and superposed on the valid diagnostic characters of the species. They are, in effect, similar, if not identical, responses of closely related species to the same environment. On the other hand, truly distinctive specific characters are those which evolve in allopatry as unique responses of the organism to its peculiar environment. The degree of divergence depends on the period and circumstances of geographic isolation and not at all on a mechanism which is triggered by the first post-isolation contact as suggested by Brown and Wilson. Divergent populations which make contact on common ground after reproductive isolation has been attained, may continue to diverge, and they probably do in some respects. The more important and stronger tendency, however, is toward convergence.[1] The basic specific characters, which evolved in allopatry, become stabilized in sympatry.

The great amount of variation and the instability of the characters or combination of characters distinguishing sympatric populations of *osilae* and *darwini* suggest that the species themselves are not stable. It is not improbable that future collecting will reveal the existence of one or more intergrading populations. Meanwhile, *Phyllotis osilae* is regarded as something less than a full species but more than the conventional subspecies; hence the binomial. Its position as an infraspecific category, however, coordinate with the comparably ill-defined *Phyllotis andium* and *P. haggardi*, is indicated by inclusion of *osilae* in the *Phyllotis darwini* complex.

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[1] This statement is not to be interpreted as a denial of the fact that many sibling species do differ most in sympatry. I myself (1960, p. 529 and pl. 5) pointed out that sympatric representatives of the cricetines *Oryzomys* (*Oecomys*) *concolor* and *O.* (*O.*) *bicolor* are easily recognized, but that some allopatric individuals of the same species may be indistinguishable. Additional examples among mammals can be cited, but nothing known of the evolution of these paired species supports the concept of "character displacement."

Sympatry also occurs between *Phyllotis darwini* and its most nearly related congeners outside the complex. The range of the western Peruvian *Phyllotis amicus* overlaps that of *P. darwini posticalis*, but nothing is known of the habits of the latter. The morphology of *P. darwini* and *P. griseoflavus* suggests some ecological segregation where they are sympatric. The two species, however, are evidently synecetic, and individuals of both have even been found in the same burrow. *P. darwini* has also been found in common collecting localities with the Patagonian *P. micropus* but it is assumed this occurs where man has altered the habitat of the second to permit invasion by the first.

Calomys, the only other undoubted polytypic phyllotine genus, comprises four species. Where their ranges overlap, *C. laucha* is the pampa mouse, while the larger *C. callosus* is restricted to gallery and scrub forests. *Calomys sorellus* and the smaller, shorter-tailed *C. lepidus* have been taken in the same localities in Peru. It is virtually certain that they, too, are ecologically segregated.

CROP VARIATION

No two generations of a population develop in the same way and at the same rate. Most common differences between generations, or crops, are in size, weight, pelage, color, reproductive rate, and population density. Such differences between generations, or seasonal crops, of the same population are expressions of *crop variation.*

The young of grazing cricetine rodents, including phyllotines, acquire adult characters and habits precociously as compared with the young of forms that undergo a prolonged development in the comparatively stable environment of maternal nest, den or burrow. Phyllotines born during the dry season are promptly exposed to rigorous living conditions. Available food may be barely sufficient to supply the young animal with energy needed for foraging and for maintaining body weight commensurate with increasing size. On the other hand, phyllotines born in the rainy season may be literally bedded in an abundance of tender shoots of succulent plants. The quantity and quality of such food, combined with the ease with which it is taken and eaten by the mouse, must contribute to development of potential maximum in size of skeletal and dental parts. Thus, an individual born and developed during the fruitful rainy season may be larger, and, because of less molar abrasion, erroneously adjudged younger, than a comparably aged product of the barren dry season.

When phyllotines of one local crop survive several seasons no doubt they tend to appear like old adults of other crops of the same locality. Few small rodents, however, live through the combined life spans of two or more successive crops. The average life span of cricetines in nature is less than six months. Blair (1948) calculated the longevity of wild living individuals of comparable Michigan *Peromyscus maniculatus*, *P. leucopus*, and *Microtus pennsylvanicus*, as varying from four to five months. Snyder (1956, p. 27), using finer methods, determined the average life span of *Peromyscus leucopus* as five months. Hence, a phyllotine may be born, reach sexual maturity, reproduce and die during the three to six months duration of a normal dry or rainy season anywhere within its range.

No field studies of crop variation in phyllotines have been made. However, results of an 11-year investigation of cyclical fluctuations in the cotton rat (*Sigmodon hispidus*) population of a fallow field in Georgia, are pertinent. The investigator, Odum (1955) found that "cotton rats appear on the runways when a week or less old . . . and begin to breed when two months or less in age. . . . Since few individuals may be expected to live more than six months, the population turnover may often be complete every six months. With a species such as the cotton rat which begins to breed at an early age and rarely lives long enough to reach maximum size it is clear that average measurements of 'adults' will vary according to the stage in the population oscillation. . . . Therefore, size should not be used as a criterion for the establishment of geographic races or subspecies unless the sample is very large and the stage in the population cycle from which it was taken is known."

A study by Martin (1956, p. 388) of a Kansas population of the prairie vole (*Microtus ochrogaster* Wagner) revealed that during an unusually dry summer reproduction was inhibited, adult voles lost weight, and young born in the spring ceased to grow. Fitch and Rainey (1956, p. 528) conducted a similar study of the eastern woodrat (*Neotoma floridana* Ord) and found that "growth rate and adult weight are influenced to a large extent by season." They did not overlook the importance of individual differences as controlling factors.

In the works cited above, organic variations are correlated with population cycles, and with seasonal changes in the quantity and quality of the food supply, temperature, and rainfall. The importance of food alone among wild brown rats (*Rattus norvegicus* Berkenhout) was determined experimentally by Calhoun (1949, pp. 1113–1122). The rats were kept in a specially designed pen. Those born near the abundant and continuously maintained food supply grew more rapidly, attained larger size, and were higher in the social order than those born farther away.

Other field studies of less nearly related mammals support the concept of crop variation. Scheffer (1955, pp. 493–513) was primarily concerned with the relationship between body size and numerical abundance in seals. He also reviewed some of the literature regarding the same relationship in the brown rat, house mouse, vole, muskrat, gray squirrel, raccoon, deer, and man. As a corollary, Scheffer noted (op. cit., p. 513) that "body size is, of course, not only a genetic product but a quantitative measure of environmental response. When certain body characters vary significantly in size from those of the generation closely removed, it may be argued that here are members of two 'races' separated only by a thin partition of time. The argument is unrealistic but it does make a point: where slight differences are critical, the systematist should choose samples for comparative study taken from similar population density environments. This precaution extends the meaning of Cazier and Bacon (1949 [Bull. Amer. Mus. Nat. Hist., **93:** 343–388]): 'The specimens should be from similar climatic, edaphic, and biotic situations . . . taken within a limited range of time so as to preclude possible confusion resulting from contamination by seasonal variance.'" Here I must interpose that the systematic mammalogist can deal only with the material at his disposal and has little or no knowledge of particular habitats or population densities. He need only learn to discount crop and other levels of intraspecific variation in evaluating the taxonomic status of the sample.

Environmental factors that combine to modify each crop are separated in *time* from those modifying the next crop. Modifications within a crop produced by environmental factors separated in *space* are discussed under the next heading.

NICHE VARIATION

Differences between individuals living in one section of the range of a population and individuals of the same species inhabiting another section of the same range are expressions of what is here termed *niche variation.* Calhoun's experiment with brown rats, cited above as an illustration of crop variation, is also a valid demonstration of one kind of niche variation. Likewise, individuals or small colonies of phyllotines living nearest the best food supply can reasonably be expected to be better developed than their neighbors not as favorably stationed. Certain phyllotines, notably *Phyllotis darwini* and *Calomys laucha*, reside in human dwellings, storehouses, well-watered gardens, refuse dumps and similar habitats with a suitable and permanent food supply. Inhabitants of such special niches can acquire somatic characters that distinguish them from members of the same population, or crop, living in natural and less favored surroundings of the immediate vicinity. Some of the striking morphological differences distinguishing neighboring colonies of tuco tucos (*Ctenomys*) and similar burrowing rodents (*Thomomys, Tachyorycles*, etc.) may be no more than manifestations of niche variation.

An investigation of house mice (*Mus musculus*) inhabiting four different environments revealed manifestations of niche variation. It was shown by Laurie (1946) that the mice in cold stores where the temperature never exceeded 15° F. lived normally, bred and produced regularly the year round, had more embryos, and were larger and heavier than mice of the other three habitats. The cold store mice ate meat exclusively. Mice of corn ricks had the highest rate of productivity, while those of urban habitats had the lowest. Mice living in flour depots were average producers. Their food consisted of white flour only. This diet may have been the cause of a skin condition characterized by thin pelage, bald patches, and torn and crumpled ears. A minority of the mice was affected and most of them lived in the same depot. The mice of the four environments were taken from a number of places in London, Oxford and other localities. For all taxonomic purposes, however, the environmentally different habitats could have been adjacent rooms in a building in Oxford where most of the urban rats were trapped.

Striking differences in color may also be manifestations of niche variation. The unusually pale color in two species of bats, *Tadarida brasiliensis* and *Myotis velifer*, living in certain Texas caves is the result, according to Constantine (1957, p. 465), of the bleaching effect of environmental ammonia gas and water vapor. Later Constantine (1958, p. 513) confirmed his conclusions by reproducing experimentally the bleaching effect of ammonia and high humidity on live *Tadarida*.

The distinction between crop and niche variation is blurred or erased in nearly all experiments in which attempts are made to determine the effects of environment on organic growth and development. Nevertheless, such experiments often produce significant differences between the test animals and sometimes suggest the kinds of differences which might exist in nature between groups of individuals of the same population separated in time or space. In one experiment, Ogle (1934a, p. 628) found that female white laboratory mice subjected to a warm (31°–33° C.), humid (75%) environment had fewer fertile matings, smaller litters and less viable offspring than mice of the same strain kept in a uniformly cool (17.8° C.) environment. The males (Ogle, 1934b, p. 635) in the warm moist room developed very short and slender bodies but the tails of each were 1 cm. longer than combined head and body length. Males acclimated in the cool room increased in body weight and length at practically the same rate as the control mice kept at 21°–27° C. Their tails, however, were 1 cm. shorter than combined head and body length. In a similar experiment by Biggers, Ashoub, McLaren and Michie (1958, p. 144), who used different hot and cold environmental temperatures, the results were generally the reverse. Females in hot (28.09° C., 87% humidity) and cold (4.78° C., 77.48% humidity) environments had a higher mortality of prenatal and postnatal young than females in the temperate or control (21° C., 69.03% humidity) environment. Furthermore, "no significant differences in rate of growth or development were found between the mice in the hot and temperate environments. Both growth and development were markedly retarded in the cold."

Changes in the gross appearance and chemical composition of the teeth of rats may also be induced by chronic exposure to adverse environments. Harris, Mefferd and Restivo (1960, p. 476) showed that the incisors in rats acclimated for 3 to 6 months at a temperature of 36° C. usually acquired a heavy reddish-brown deposit. The incisors in rats maintained at a high altitude (380 mm. Hg.) remained normal. Food intake, hence masticatory activity, was approximately the same in the heat and altitude groups. Rats exposed to a combination of heat and high altitude revealed significantly reduced concentrations of calcium, phosphate and magnesium in their incisors.

As a final example, Harrison (1958, p. 892) investigated such characters as longer tails, larger feet, thinner pelage, smaller body size and general acclimatization of mice (*Mus musculus*) subjected to a hot environment by a number of experimenters including Ogle (1934b, p. 635), mentioned above. Harrison concluded (p. 900) "that at least some of the changes, both physiological and morphological, which occur when mice are reared at high temperatures, are in their over-all effect adaptive."

Trapping of mice for taxonomic studies is almost always limited in time and restricted in place. The sampling of any species thus secured is often representative of only one crop and/or niche. Sometimes a few survivors of an older crop, or strays from a different niche, may be included in the sampling. Such individuals help form a more nearly exact concept of variation within the species. Occasionally crop and niche variants are mistakenly adjudged distinct species or perhaps sympatric(!) subspecies.

SOCIABILITY

Most phyllotines are social or gregarious and many are commensal as well. Darwin (*in* Waterhouse, 1839, p. 44) reported that six specimens of the type series of *Hesperomys bimaculatus* (= *Calomys laucha*) were discovered in the same burrow. The social and gregarious habits of *Phyllotis sublimis* were observed by Pearson (1951, p. 147), and Thomas (1900, p. 467) noted that the type and eight topotypes were dug out of one hole. Because of their preeminently grazing habits, populations of species of *Phyllotis, Andinomys edax, Chinchillula sahamae* and, possibly, *Galenomys garleppi*, tend to concentrate in the midst of localized stands of the more succulent grasses.

In some cases, sociability develops into colonialism through commensalism. Small populations of *Phyllotis darwini* become integrated with colonies of tuco tucos (*Ctenomys*) or cavies (*Cavia, Galea*, and others) by sharing their living quarters and feeding grounds. Individuals of *Phyllotis darwini* have also been found in the same burrows with *Octodon degus, O. bridgesi, Abrocoma bennetti, Akodon olivaceus, Abrothrix longipilis, Oryzomys longicaudatus, Rattus rattus,* and *Marmosa elegans* (fide Wolffsohn *in* Thomas, 1927, p. 556). Pearson (loc. cit.) noted *Phyllotis boliviensis* living in a viscacha colony and *P. sublimis* sharing homes with nearly every other cricetine of the same region in the Peruvian *altiplano*. De la Barrera (1940, p. 572) records *Phyllotis griseoflavus* and *P. darwini* each living together with *Microcavia australis* in burrows of the latter in Mendoza, Argentina.

Sociability in phyllotines is not restricted to natural habitats. *Phyllotis darwini, P. griseoflavus, Calomys laucha* and *C. callosus* are common tenants of man's habitations, where they compete successfully with the introduced commensals *Rattus* and *Mus*.

Nothing is known of the habits of the highly localized Piura desert mouse *Phyllotis gerbillus*. The ease with which the collector Celestino Kalinowski secured a series of 17 topotypes suggests, however, that this species is gregarious, like most of its relatives. On the other hand, there is nothing in the records of *Eligmodontia typus* to indicate that this gerbil-like mouse is anything but solitary outside the breeding periods.

RATADAS AND PLANT FRUITING CYCLES

Devastations of cultivated fields and store rooms and invasions of human habitations and villages by inordinately large numbers of hungry rodents are termed *ratadas* in most parts of rural South America. The expression *rat plague* refers to the same phenomenon but has been used interchangeably with the differently meaning *bubonic plague*. *Ratadas* are commonplace in South America and a number of them have been recorded. Only exceptionally were the rodents involved identified. It is certain, however, that phyllotines, notably the ubiquitous species of *Phyllotis* and *Calomys*, are among the anonymous "mice" of many *ratadas* mentioned in the literature.

Ratadas originate in restricted localities when an extraordinary surplus of natural food, usually the fruit of one or two kinds of plants, occurs together with ideal cover and nesting sites for mice. In this environment multiplication of the population of one or a few species of mice assumes explosive proportions, and the number of individuals soon exceeds by many times the ordinary carrying capacity of the range. With termination of the fruiting season and deterioration of protective cover, the hungry, exposed rodents break out into the surrounding countryside. By the time a new balance is reached between the individual and its range, there has been a precipitous drop in the rodent population and considerable destruction of the cultivated crops in the overrun area. The many dead mice often observed after a *ratada* peak are the victims of exposure, hunger, thirst, abnormally vicious inter- and intra-specific competition, cannibalism, and wholesale killing by man and predator. Sometimes disease strikes the rodents with catastrophic effects. Another cause of high mortality may be the radical change in diet for the generations of mice that developed chiefly, if not entirely, after weaning, on one plant food.

In many parts of South America *ratadas* are correlated with the fruiting of diverse species of bamboo. One of the earliest recorded took place in Valdivia, Chile, in 1780. This *ratada* is cited by Philippi and Landbeck (1858, pp. 81–82) from a manuscript written by the historian and naturalist Claudio Gay. The manuscript adds that periodic plagues of *pericotes* (native name for small rodents in general, and often for *Phyllotis darwini* and *Rattus* in particular) scourged all parts of Chile. The *ratadas* were known to occur in cycles of 17 to 20 years that coincided with the cyclic fruiting and dying of the "coligue," a bamboo used by the Indians for lance shafts. Philippi and Landbeck (op. cit.) also mention a sudden outbreak of rats in the Araucanian districts of southern Chile, in 1681. No explanation is given for the *ratada* and no source for the reference. However, in 1869 or 1870, Philippi (1879) observed a *ratada* in Valdivia, where he was in residence. On that occasion all the "coligue" bamboos of the province produced seed at the same time and died immediately thereafter. Philippi noted also that *ratadas* occur "sometimes in the south of Chile, Araucania, Valdivia, and Llanquihue, when the coligue and other species of *Bambuseae* have flourished and fructified, an occurrence which happens every 15–20 years." The common native mice that might have participated in these *ratadas* are species of *Phyllotis, Akodon* and *Oryzomys nigripes* (=*longicaudatus*). According to Schneider (1946, p. 77), *Oryzomys nigripes* was probably the species which devastated the fields of Concepción Province, Chile, during the notorious *ratada* of July, 1877.

The best account on the subject of the correlation between *ratadas* and the fruiting season of certain species of bamboos was provided by Orville A. Derby (1879, p. 65): "From time to time in all parts of Brazil the plantations are subject to the depredations of armies of rats that issue from the forests and consume everything edible that comes in their way. During a recent excursion in the province of Paraná Mr. Derby found an almost universal lack of corn throughout the province, due to such invasion of rats, by which almost the entire crop of last year had been destroyed. This invasion, or plague as it is called, is said to occur at intervals of about thirty years, and to be simultaneous with the drying of the *taquara*, or bamboo, which everywhere abounds in the Brazilian forests. The popular explanation is that every cane of bamboo sprouts with a grub, the germ of a rat, within it, and that when the bamboo ripens and dies the germ becomes a fully-developed rat and comes out to prey on the plantations. An educated and observant Englishman, Mr. Herbert H. Mercer, who has resided a number of years in the province and had an opportunity of studying the phenomenon, furnished Mr. Derby the following rational and curious explanation: The bamboo arrives at maturity, flowers and seeds at intervals of several years, which doubtless vary with the different species. The period for the species most abundant in Paraná is thirty years. The process, instead of being simultaneous, occupies about five years, a few of the canes going to seed the first year, an increased number the second, and so on progressively, till finally the remaining and larger portion of the canes seed at the same time. Each cane bears about a peck of edible seed, resembling rice, which is very fat and nourishing, and is often eaten by the Indians. The quantity produced is enormous, and large areas are often covered to a depth of five or six inches. After seeding the cane dies, breaks off at the root and falls to the ground, the process of decay being hastened by the borings of larva which live upon the bamboo and appear to be particularly abundant at seeding time. These larva have doubtless given rise to the story of the grub developing into a rat. New canes spring up from the seed, but require seven or eight years to become fit for use, and thirty to reach maturity. With this sudden and constantly increasing supply of nourishing food for a period of five years, the rats and mice, both of native and imported species, increase extraordinarily in numbers. The fecundity of these animals is well known, and the result after four or five years of an unusual and constantly increasing supply of excellent food and in the absence of enemies of equal fecundity, can readily be imagined. The last of the crop of seed being mature and fallen to the ground, the first rain causes it to decay in the space of a very few days. The rats, suddenly deprived of food, commence to migrate, invading the plantations and houses and consuming everything that does not happen to be repugnant to the not very fastidious palate of a famishing rodent. If this happens at the time of corn planting, the seed is consumed as fast as it can be put into the ground. Mr. Mercer, who plants annually about fifty acres of corn, replanted six times last year, and finally gave up in despair. The mandioca is dug up; the rice crop, if it happens to be newly sown or in seed, is consumed, as is also everything in the houses in the way of provisions and leather, if not carefully guarded in tin trunks."

The 30-year blooming cycle of the *taquara* and its correlation with *ratadas* was corroborated by Pereira (1941). The plant was identified as the *taquara lixo* (rough bamboo, *Merostachys fistulosa* Doell). Pereira also reviewed part of the history of *ratadas* in southern Brazil, beginning with a citation of observations made by the French botanist, August St. Hilaire, in 1832 (Voyage dans l'interieur du Brésil). Giovannani, Vellozo and Kubiak (1946) continued the investigation of *ratadas* in Paraná. This time the outbreak was correlated with the fruiting of the *taquara lisa* (smooth bamboo, *Merostachys* sp.). Here, again, exhaustion of their food supply in the bamboo groves obliged the mice to erupt into the neighboring cultivated fields. The species involved in this *ratada* included the phyllotine *Calomys laucha tener* Wagner, and *Oryzomys nigripes* Olfers (*Oryzomys eliurus* Wagner), *Holochilus brasiliensis leucogaster* Brandt and *Akodon nigrita* Lichtenstein (the *rato pitoco*).

Crespo (1944) studied a *ratada* of *Calomys laucha laucha* Olfers and *Akodon benefactus* Thomas that developed in fallow fields on the outskirts of Buenos Aires, Argentina. In this case, prolonged warm weather and heavy rainfall stimulated superproduction of natural food and heavy growth of cover favored by the mice. An abrupt change to abnormally dry, cold weather destroyed forage and cover, and obliged the rodents to invade adjoining cultivated fields.

A *ratada* in south coastal Peru was investigated by Gilmore (1947). Though the affected area lies within the range of *Phyllotis darwini*, Gilmore found that only the *rata-muca* (*Oryzomys xanthaeolus ica* Osgood) was involved. The cause for the outbreak was not determined.

I have found the phyllotine *Zygodontomys brevicauda* in near plague numbers in some northern Colombian localities. I also encountered other South American rodents, notably the forest dwelling *Oryzomys laticeps* and *Oryzomys caliginosus*, some species of *Thomasomys*, the spiny rat *Proechimys guyannensis*, and the grassland *Heteromys anomalus* and *Sigmodon hispidus*, in excessive numbers. The history of *ratadas* of marsh rats (*Holochilus*) was recorded elsewhere (Hershkovitz, 1955, p. 655).

The meager data in literature, and personal observations in the field, indicate that fluctuations in populations may be as drastic in tropical and south temperate latitudes as in Arctic and north temperate ones. *Ratadas* in the Neotropical region are usually composed of one, sometimes two, rarely more, species of the local rodent fauna. Environmental conditions that promote the production of a *ratada* of one species may not alter significantly the population of another species living in the same area. The one or two species least affected by adverse conditions in a given locality are most likely to become plagues during optimum conditions. Species able to thrive in newly invaded territory are also notoriously *ratada*-prone.

HIBERNATION

Hibernation, or aestivation, as a regular seasonal function, has not been positively demonstrated in any South American mammal. There are suggestions, however, that sloths and certain small Patagonian marsupials, bats, a marmoset[1] and rodents may become torpid at irregular intervals. The mouse opossums, *Marmosa pusilla* (=*elegans*) and *Dromiciops australis*, store fat in their bodies, notably at the base of the tail, in advance of winter and become lethargic during particularly cold spells. Some phyllotines are also prone to torpidity when the outside temperature is low. One of the *lauchas* secured by Thomas (1916b, p. 184) in Buenos Aires province during the winter month of June, 1896, is said to have been "dug up, semi-torpid, in very cold weather, from about 6 inches below the surface of the ground." The species (described as *Hesperomys murillus*, a synonym of *Calomys laucha laucha*) is not a burrower and Thomas does not explain its presence underground or state that he himself found it there. Henry Durnford (*in* Thomas, 1898a, p. 210) observed that whereas *Phyllotis griseoflavus* was excessively numerous and overran the Colony in Chubut, Argentina, during the summer, it disappeared in the wintertime. Durnford believed that the animal became dormant. Pearson (1951, p. 147) also puzzled over the sudden disappearance of *Phyllotis sublimis* Thomas from the Peruvian *altiplano* during the rainy season months of October, November and December. However, in regions where the most drastic environmental change is in rainfall, not temperature, absence of trap or sight records need not be the result of hibernation. A lush growth of food cover plants during the rainy season makes mice sedentary, less exposed to predators and less, if at all, trap prone (see also discussion of *Ratadas*, p. 42).

ENEMIES

Phyllotines, together with *Akodon* (sens. lat.), are the dominant mammals of the grasslands, scrublands and deserts of South America. As such they are basic food for the carnivores living in the same range. The most important predators include the weasel (*Mustela frenata*), the huron (*Grisonella*), species of foxes and wild cats, owls and hawks. In tropical savannas inhabited by *Zygodontomys*, snakes feed largely on small rodents.

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[1] *Callithrix jacchus*, in captivity (Kraft, 1957, Säugeth. Mitt., **5**: 175).

Precocious development and the short suckling period of young phyllotines help reduce loss of population to nest-raiding predators.

ECTOPARASITES

The distributional patterns of ectoparasites often provide important clues to the origin and phylogeny of their mammalian hosts. Modern parasitologists explore this relationship, and notable contributions on the subject have already been made by many investigators. In addition to those cited below, the works of Hopkins and Rothschild (1953–56) and Johnson (1957) on fleas (*Siphonaptera*) may be consulted to advantage. Ferris and Stojanovich (1951) monographed sucking lice (Anoplura) and Vanzolini and Guimaraes (1955) have discussed the geographic distribution and host associations from a historical point of view.

Few studies have been made of the ecological relationship between disease-transmitting ectoparasites and Neotropical rodents. The most outstanding are those of de la Barrera. One of his works on sylvatic plague and life histories of rodent vectors is cited below; others are mentioned in the present account of *Phyllotis griseoflavus* (pp. 441–461).

A list of some of the fleas, lice, mites, ticks and staphylinid beetles infesting phyllotines is given herewith. The authorities for published records are shown in parentheses following the name of the parasite. Heretofore unpublished records of specimens in Chicago Natural History Museum are distinguished by the symbol CNHM. The identifications were made by Dr. Rupert Wenzel, Curator of Insects of this institution, who also checked the nomenclature of all parasites listed. An interrogation(?) sign before the name of a parasite means that the host association is doubtful.

Host names given below are those recognized in the revision. For concordance between host names originally used by the parasitologists cited and those adopted here, see the synonymies and geographical distributions in the text that follows.

CALOMYS Section

Calomys sorellus Thomas
  Tick
    Ixodes (Exopalpiger) andinus Kohls (CNHM)

Calomys laucha Olfers
  Fleas

Polygenis rimatus Jordan (Costa Lima and Hathaway, 1946)
Craneopsylla minerva wolffhuegeli Rothschild (Hopkins and Rothschild, 1956)

Calomys lepidus lepidus Thomas
Fleas
(?)*Plocopsylla pallas* Rothschild (Hopkins and Rothschild, 1956)
(?)*Tetrapsyllus bleptus* Jordan and Rothschild (Traub, 1952)
(?)*Neotyphloceras crassispina crassispina* (CNHM)
(?)*Agastopsylla nylota* (CNHM)
(?)*Sphinctopsylla inca* Rothschild (Hopkins and Rothschild, 1956)
(?)*Dysmicus claviger* Rothschild (Johnson, 1957)

Calomys callosus Rengger
Lice
Hoplopleura hesperomydis Osborn (Hopkins, 1949; Ferris, 1919–35)
Hoplopleura nesoryzomydis Ferris (Hopkins, 1949)
Hoplopleura affinis Burmeister (Ferris, 1919–35)

Flea
Craneopsylla minerva wolffhuegeli Rothschild (Hopkins and Rothschild, 1956)

Calomys callosus expulsus Lund
Flea
Polygenis bohlsi bohlsi Wagner (Costa Lima and Hathaway, 1946)

Zygodontomys lasiurus Lund
Louse
Hoplopleura affinis Burmeister (Hopkins, 1949)

Zygodontomys brevicauda J. A. Allen and Chapman
Louse
Hoplopleura nesoryzomydis Ferris (Hopkins, 1949)

PHYLLOTIS Section

Phyllotis haggardi Thomas
Flea
Nosopsyllus londiniensis Jordan (Johnson, 1957)

Phyllotis andium Thomas
Flea
Craneopsylla minerva minerva Rothschild (CNHM)

Tick
Ixodes (*Exopalpiger*) *andinus* Kohls (CNHM)

Beetle
Amblyospinus ancashi Seevers (Seevers, 1955)

Phyllotis darwini posticalis Thomas
Fleas
(?)*Plocopsylla pallas* Rothschild (Hopkins and Rothschild, 1956)
(?)*Dysmicus claviger* Rothschild (Johnson, 1957)
Neotyphloceras crassispina crassispina Rothschild (CNHM)
(?)*Agastopsylla nylota* Traub (Traub, 1952)

    - (?)*Tetrapsyllus bleptus* Jordan and Rothschild (Traub, 1952)
    - *Cleopsylla townsendi* Rothschild (CNHM)
  - Tick
    - *Ornithodoros* sp., larvae (CNHM)

- *Phyllotis darwini rupestris* Gervais
  - Fleas
    - *Delostichus phyllotis* Johnson (Johnson, 1957)
    - *Neotyphloceras crassispina crassispina* Rothschild (CNHM; Traub, 1952; Costa Lima and Hathaway, 1946)
    - *Tetrapsyllus bleptus* Jordan and Rothschild (CNHM)
    - (?)*Polygenis byturus* Jordan and Rothschild (Costa Lima and Hathaway, 1946)
    - *Plocopsylla inti* Johnson (Johnson, 1957)
    - *Sphinctopsylla inca* Rothschild (Johnson, 1957)
  - Louse
    - *Hoplopleura affinis* Burmeister (Hopkins, 1949)
  - Mite
    - *Euschongastia phylloti* Wharton (Wharton, 1948)
  - Tick
    - *Ornithodoros* sp., larvae (CNHM)

- *Phyllotis darwini darwini* Waterhouse
  - Fleas
    - *Neotyphloceras crassispina chilensis* Jordan (Costa Lima and Hathaway, 1946)
    - *Plocopsylla wolffsohni* Rothschild (Costa Lima and Hathaway, 1946; Hopkins and Rothschild, 1956)
    - *Cleopsylla townsendi* Rothschild (Johnson, 1957)

- *Phyllotis darwini xanthopygus* Waterhouse
  - Fleas
    - *Plocopsylla chiris* Jordan (Costa Lima and Hathaway, 1946; Hopkins and Rothschild, 1956)
    - *Plocopsylla achilles* Rothschild (Costa Lima and Hathaway, 1946)
    - *Tiamastus subtilis* Jordan and Rothschild (Costa Lima and Hathaway, 1946)
    - *Craneopsylla minerva wolffhuegeli* Rothschild (Hopkins and Rothschild, 1956)
    - (?)*Polygenis byturus* Jordan and Rothschild (Johnson, 1957)
    - *Tiamastus subtilis* Jordan and Rothschild (Johnson, 1957)

- *Phyllotis osilae* J. A. Allen
  - Flea
    - (?)*Polygenis thurmani* Johnson (Johnson, 1957)

- *Phyllotis micropus* Waterhouse
  - Lice
    - *Hoplopleura affinis* Burmeister (Hopkins, 1949)
    - *Hoplopleura reducta* Ferris (Hopkins, 1949)

- *Phyllotis boliviensis* Waterhouse
  - Flea
    - *Cleopsylla townsendi* Rothschild (Johnson, 1957)
    - *Neotyphloceras crassispina crassispina* Rothschild (CNHM)

Louse
  Hoplopleura affinis Burmeister (Hopkins, 1949)

Phyllotis sublimis Thomas
  Flea
    Craneopsylla minerva minerva Rothschild (Johnson, 1957)

  Beetle
    Amblyopinus sp. (Seevers, 1955)

Phyllotis pictus Thomas
  Fleas
    (?)*Agastopsylla pearsoni* Traub (Traub, 1952)
    (?)*Plocopsylla enderleini* Wagner (CNHM)
    Cleopsylla townsendi Rothschild (CNHM)
    Sphinctopsylla inca Rothschild (CNHM)
    Neotyphloceras crassispina crassispina Rothschild (CNHM)
    Ectinorus ineptus Johnson (Johnson, 1957)

  Louse
    Hoplopleura affinis Burmeister (Hopkins, 1949)

  Tick
    Ixodes sp. nymphs (CNHM)

Phyllotis griseoflavus griseoflavus Waterhouse
  Fleas
    Craneopsylla minerva wolffhuegeli Rothschild (Costa Lima and Hathaway, 1946; Johnson, 1957)
    Dysmicus barrerai Jordan (Costa Lima and Hathaway, 1946)
    Dysmicus hapalus Jordan (Costa Lima and Hathaway, 1946)
    Hectopsylla stomis Jordan (Costa Lima and Hathaway, 1946)
    "*Polygenis litargus puelche* Del Ponte and Reisel" *nomen nudum* (Costa Lima and Hathaway, 1946)
    Polygenis occidentalis Cunha (Costa Lima and Hathaway, 1946)
    Polygenis platensis cisandinus Jordan (Costa Lima and Hathaway, 1946)
    Pulex irritans Linnaeus (Costa Lima and Hathaway, 1946)
    Neotyphloceras crassispina hemisus (Jordan, *in* de la Barrera, 1940)

  Louse
    Hoplopleura affinis Burmeister (Hopkins, 1949)
    Hoplopleura reducta Ferris (Ferris, 1919–35)

Phyllotis amicus Thomas
  Fleas
    Neotyphloceras crassispina Rothschild (Costa Lima and Hathaway, 1946)
    Rhopaplopsyllus cacicus Jordan and Rothschild (Traub, 1952)

Andinomys edax Thomas
  Fleas
    Dysmicus budini Jordan and Rothschild (Costa Lima and Hathaway, 1946)
    Neotyphloceras crassispina hemisus Jordan (Costa Lima and Hathaway, 1946)
    (?)*Ectinorus disjugis* Jordan (Johnson, 1957)

Chinchillula sahamae Thomas
- Fleas
  - *Cleopsylla townsendi* Rothschild (Johnson, 1957)
  - *Neotyphloceras crassispina crassispina* Rothschild (Traub, 1952)
  - *Tetrapsyllus bleptus* Jordan and Rothschild (Traub, 1952)
  - *Plocopsylla enderleini* Wagner (CNHM)
  - (?)*Agastopsylla pearsoni* Traub (Traub, 1952)
- Mite
  - *Euschonygastia phylloti* Wharton (Wharton, 1948)
- Beetle
  - *Amblyopinus* sp. (Seevers, 1955)

Euneomys chinchilloides Waterhouse
- Fleas
  - *Barreropsylla excelsa* Jordan (Johnson, 1957)
  - *Plocopsylla wolffsohni* Rothschild (Johnson, 1957)
  - *Ectinorus onychius onychius* Jordan and Rothschild (Johnson, 1957)
  - *Tetrapsyllus rhombus* Smit (Johnson, 1957)

SOME SPECIAL EXTERNAL AND CRANIAL CHARACTERS

Feet

Figure 3

The hind feet of all phyllotines except *Pseudoryzomys* are small, generally weak in structure, and adapted primarily for locomotion on the ground. Most species are good climbers but in none is the foot obviously specialized for an arboreal habitat.

The hind foot of *Pseudoryzomys* has evolved into the natatorial type, characterized by stout proportions, reduction of outer toes, weak claws, development of interdigital webbing—most markedly between the middle digits—the absence of superfluous hair, particularly from the plantar surface of the heel, and obsolescence of the fifth (outer posterior) postdigital plantar tubercle (fig. 53).

The hind foot of *Zygodontomys* also departs somewhat from the usual vole-like phyllotine structure and approaches that of the palustrine type charactersitic of terrestrial species of *Oryzomys*. The foot is stout, fan-shaped, often dark, with relatively thick, long claws and short, thin, digital bristles.

The most remarkable adaptation is the spade-shaped, gerbil-like hind foot of *Eligmodontia*. The form of the extremity and the hairy cushion of its sole are unique among cricetines. That *Eligmodontia*

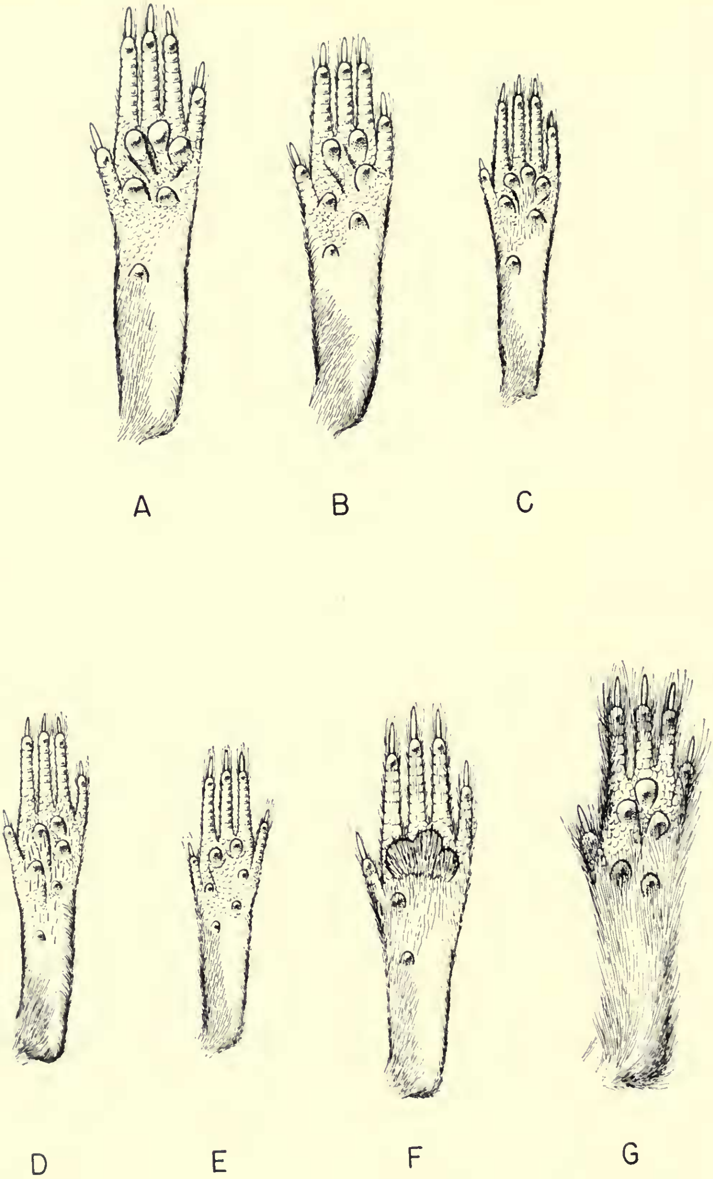


FIG. 3.—Plantar surface of left hind foot in dry skin: A, *Phyllotis darwini;* B, *P. pictus;* C, *P. gerbillus;* D, *P. amicus;* E, *Calomys* spp.; F, *Eligmodontia typus;* G, *Galenomys garleppi.*

is a desert jumping mouse is inferred from the structure of its limbs and knowledge of its habitat.

The hairy heel in phyllotines and a scattering of hairs between the plantar tubercles in some species are secondary developments, presumably adaptive, that partially replace the primitive scaly armor. The extremely hairy sole of *Galenomys* may be correlated with the cold climate of its Andean habitat, but sympatric phyllotines are not so benefited. In a like manner the sole of *Phyllotis gerbillus*, of the Piura desert, possesses an appreciable covering of bristles while that of other coastal desert phyllotines is bare.

The fifth hind digit of all species of the genus *Phyllotis* is sufficiently elongated to be of assistance in climbing. The species of *Calomys* are similarly endowed, but their hind foot is extremely delicate (fig. 38). The hind foot of *Andinomys, Chinchillula* and *Galenomys* is of the ambulatory type common to savanna species, but nothing definite is known regarding locomotion in these genera.

The hind feet of most phyllotines are remarkably uniform in structure, but the same types are common to unrelated cricetines inhabiting savanna or scrub country. The feet of *Eligmodontia, Pseudoryzomys, Zygodontomys,* and *Galenomys* are divergent from the generalized form but here, too, similar structures have evolved independently in other murids.

The forefoot of cricetines is smaller and proportionately shorter than the hind foot, and its first digit is greatly reduced. The pollex bears a nail in phyllotines and all other cricetines except the specialized fossorial forms (*Notiomys, Blarinomys, Oxymycterus, Scapteromys*) where it is provided with a claw. After locomotion the principal functions of the forefoot are the seizure and conveyance of food to the mouth. The forefoot may develop exceptionally long claws for digging in some non-phyllotines, but it shows no specializations for a particular mode of locomotion comparable in degree to those of the hind foot.

Tail

Tail length approximately equal to combined head and body length is characteristic of the more generalized, terrestrial cricetines. In a plastic, wide-ranging form like *Phyllotis darwini*, tail length varies from about one-third less to two-fifths more than head and body length. A tail with this variability adapts itself easily to terrestrial, fossorial, scansorial, saltatorial and semi-aquatic modes of life. The specialized tail, whether consistently longer or shorter than combined head and body length, can easily be derived from the flexible, medium length, all-purpose type. Tails of vole-like, burrowing *Phyllotis sublimis, Calomys lepidus, Galenomys garleppi* and *Chinchillula sahamae,* are one-third to three-fourths of the head and body length. Tails of the less specialized *Andinomys edax, Phyllotis micropus, P. boliviensis, P. pictus, Zygodontomys, Calomys laucha, C. sorellus* and *C. callosus* average between 75 and 100 per cent of head and body length.

Highly specialized saltatorial rodents may be of the bipodal or leporid type, with tail very short or vestigial, or they may be of the tripodal or ricochetal type (cf. Hatt, 1932, pp. 602 et seq.), with tail stoutly developed and, with rare exceptions, longer than combined head and body length. No cricetine belongs definitely to either saltatorial category, but *Eligmodontia* shows a slight tendency toward the second. The elongated, tufted, balancing type of tail of scansorial or arboreal rodents is found in *Phyllotis griseoflavus* and *P. amicus.*

In specialized, short-tailed forms, the tail of juvenals is always proportionately longer to head and body length than in adults. On the other hand, the tail of young individuals of long-tailed species is usually proportionately shorter.

Bony Palate

Figure 4

The postdiastemal portion of the hard palate of nearly all cricetine species may be classified as short or long and as wide or narrow. These terms are defined as follows:

Short palate: With median posterior borders of palatines not extending behind posterior plane of third molars.

Long palate: With median posterior borders of palatines extending behind posterior plane of third molars.

Wide palate: With distance between inner borders of first molars greater than length of either molar.

Narrow palate: With distance between inner borders of first molars less than length of first molar. In many cases the narrow palate is marked by a pair of deep lateral troughs separated by a prominent median longitudinal ridge. These features indicate that the narrow palate derives from a longitudinal corrugation of the wide palate.

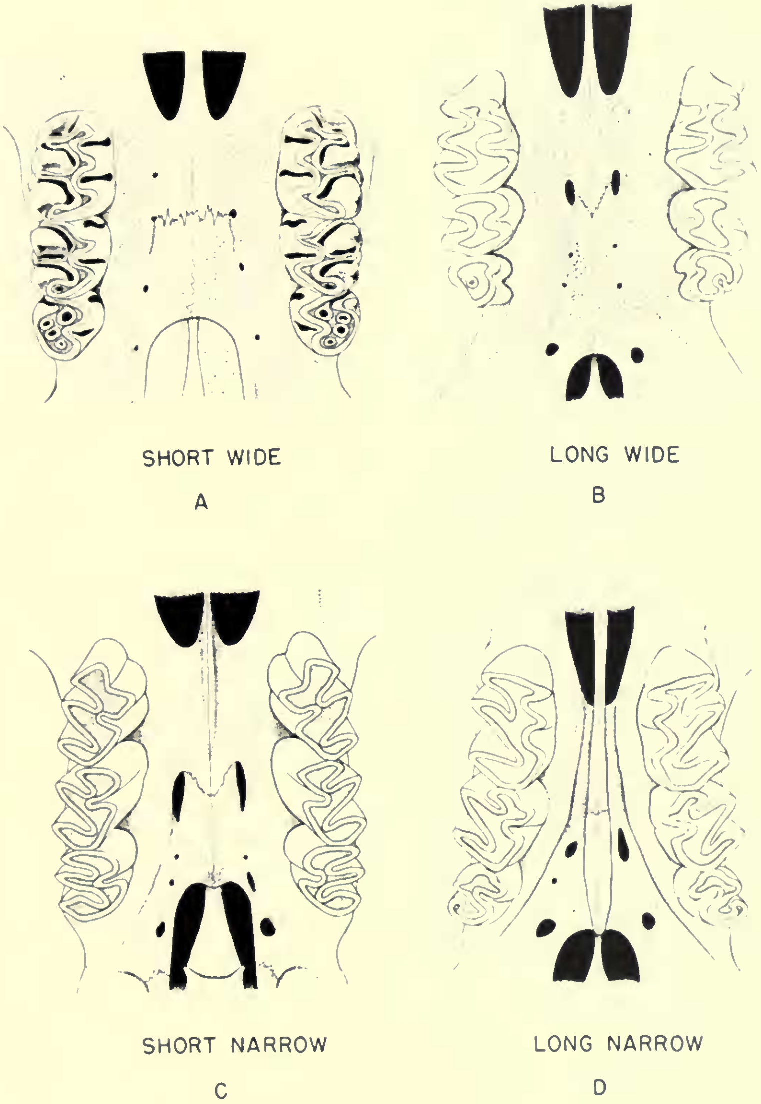

SHORT WIDE
A
LONG WIDE
B
SHORT NARROW
C
LONG NARROW
D

FIG. 4.—Hard palates in Muridae: A, short, wide (*Thomasomys*); B, long, wide (*Phyllotis*); C, short, narrow (*Neotoma*); D, long, narrow (*Andinomys*). Molars pentalophodont in A, and derivatives of the tetralophodont pattern in B–D.

The wide, short, uncomplicated palate such as occurs in *Peromyscus* (s.s.), most species of *Thomasomys* (fig. 4, A), *Rhipidomys* and other related genera, is here regarded as primitive. Brachyodont, bunodont molars, whether pentalophodont or tetralophodont, are commonly associated with the wide, short, simple palate. On the other hand, the narrow palate, either long or short, is rarely associated with the generalized or low crown, crested molars of cricetines. In a few forms (e.g., *Irenomys*) the palate has remained primitively short but is clearly evolving from wide to narrow, while the molars have already reached an advanced stage of hypsodonty and lamination. A clearly defined narrow and short palate, however, does not appear in any South American cricetine. Among North American peromyscines, the palate of woodrats (*Neotoma, Xenomys*) is narrow and short (fig. 4, C) and may become even shorter as it constricts *pari passu* with increasing hypsodonty.

The long, postdiastemal portion of the palate evolved from the short, wide palate by a closing of most of the gap between the median posterior portions of the paired palatine bones. It represents completion of the roofing-over process of the secondary or mammalian palate and is always correlated with complications of the posterior palatal and postpalatal regions. The evolutionary stages are evident in living forms. Thus in juvenals with unerupted third molars this type of palate is still simple and comparatively short. In akodonts and such peromyscines as *Haplomylomys, Podomys, Baiomys, Reithrodontomys* the palate is wide, with a narrow range of variation from short to long. Usually, the posterior palatal area in this group is inflated, and the pits are roofed (as seen from below). The wide palate of the dentally primitive *Aporodon* also varies from short to barely long. In phyllotines (fig. 4, B), the postdiastemal portion of the palate is consistently long and is distinguished by the presence of more or less conspicuous posterolateral palatal pits or fossae. Here the palate is wide in all genera except *Andinomys* and *Chinchillula*. It is widest in the brachyodont, bunodont *Calomys, Eligmodontia,* and *Zygodontomys* and becomes progressively narrower with increasing hypsodonty. The narrow palate in *Andinomys* (fig. 4, D) and *Chinchillula* is associated with extremely high, flat-crowned molars.

The palate of sigmodonts (*Holochilus, Sigmodon, Neotomys, Reithrodon*) is generally wide; the molars, however, are more advanced than those of phyllotines and the postpalatal pterygoid region is extremely complicated.

The palate of oryzomyine rodents is definitely long and like the wide type of most phyllotines. Identical palatal structures in buno-brachy-pentalophodont oryzomyines and buno-brachy-tetralophodont phyllotines may be independent developments or may point to a common ancestry.

A primitive palate may be associated with any advanced stage of evolution in other cranial, dental, and external characters. Conversely, a specialized palate may be associated with generalized characters in other parts of the organism. The structure of the palate alone, however, tends to be constant or to vary in but one direction in any given species or genus.

The combination of postdiastemal palatal and molar characters is an important indicator of generic and supergeneric relationships. The accompanying diagram (fig. 2) shows the palatal-molar relationship between phyllotines and those cricetine groups with which comparisons are made.

Proportional length of the diastemal portion of the palate, whether long or short, is also an important character in the systematics of the Muridae, as well as in other rodent groups. However, among phyllotines and most pastoral cricetines in general, the character is of little significance. A discussion of its implications, therefore, is omitted here. In another section (p. 102) the elongated type of the diastemal portion of the palate is mentioned in connection with dental specializations and feeding habits.

Supraorbital Region

Figure 23

In most phyllotines, as in *Muridae* in general, the borders of the supraorbital region are either divergent or concave mid-frontally. In some, the sides of the supraorbital region vary from parallel to concave or divergent. In the concave type, the distance across the sides of the supraorbital region, measured at the mid-frontal plane, is always less than the greatest width of the rostrum. In the divergent type, the width across the sides is always more. The primitive murid supraorbital region was almost certainly of the concave type but with sides nearly parallel mid-frontally. This condition persists in many cricetines and in the phyllotine *Calomys lepidus*, *Phyllotis darwini* and others. In *Calomys sorellus* the sides vary from slightly concave to parallel mid-frontally, while in *Calomys laucha* the sides vary from parallel to slightly divergent.

The supraorbital regions of juvenals of either type is generally broad without notable constriction or divergence. In adults specialization of the supraorbital region has led either to further constriction of the concave type with formation of longitudinal frontal ridges or to greater expansion of the divergent type with development of beading and overhanging frontal ledges. Exaggeration of either the concave or the divergent type of supraorbital region is also characteristic of old age.

Tendency toward constriction of the supraorbital region is present but hardly noteworthy in *Phyllotis pictus* and *P. boliviensis.* In closely related *Euneomys chinchilloides,* and in sigmodonts like *Reithrodon physodes, Neotomys ebriosus,* and *Holochilus magnus,* there is marked constriction. Extreme constriction of the supraorbital region is attained in microtines.

Increasing expansion of the divergent type of supraorbital region may be traced in phyllotines from the nearly parallel, square-sided condition in *Calomys laucha* to the widely divergent, beaded, ledge-like supraorbital borders in *Calomys callosus, Zygodontomys* and *Phyllotis griseoflavus.* As in the concave type, development of divergent-sided supraorbitals has not gone far in phyllotines. Most advanced conditions among other cricetines appear in arboreal forms such as *Tylomys, Ototylomys, Nyctomys* and the *Oecomys* section of *Oryzomys.* The correlation between an arboreal habitat and a divergent-sided supraorbital region appears in Old World Muridae as well.

There is no apparent reason for the predominance of the expanded, divergent-sided type of supraorbital region among scansorial and arboreal species of Muridae (including Cricetinae). Also, no explanation is offered for the greater prevalence of the constricted concave type of supraorbital region among voles and vole-like mice. In either case, modification of the supraorbital regions appears to be of specific rather than generic grade.

Baculum

Figures 5–8

The two basic types of bacula, simple and complex, are defined and their systematic significance is discussed in a preceding section (p. 19).

The baculum of all phyllotines of which the element has been studied is complex (figs. 5, B; 6). This type is characterized by a bony shaft with an expansion at the base and three soft, cartilaginous or more or less ossified, digitate processes at the tip. The base (fig. 6) is marked by a pair of lateral condyles that are thickened or knobby in some specimens, undercut or channeled and curled upward in others. The condyles may be connected along the median line by an expanse of bone or they may be separated by a median incision.

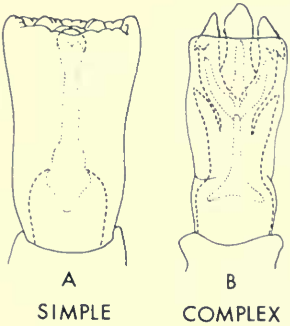


FIG. 5.—Simple and complex types of glandes pene and bacula. A, glans penis and baculum (dotted) of *Baiomys musculus* (after Hooper [1959, pl. 4*a*]); B, glans penis and baculum (dotted) of *Phyllotis darwini.*

The basal contour of the shaft varies from either concave or convex to nearly plane.

Shafts with the convex base predominate among cricetines with the complex type of bacula. The same shape of base appears to be universal among microtines and in cricetines with the simple type of baculum and glans.

The concave base (figs. 5, 6) is found only in *Phyllotis darwini* among strictly South American cricetines, and Burt (1960, pl. 24*a*) figures the baculum of only one North American species, *Oryzomys alfaroi,* with the same kind of base. The base of the nearly related *Oryzomys melanotus,* figured by the same authority (pl. 24*e*) is convex.

Bacula of juvenals of phyllotine species with either convex or concave bases, are practically indistinguishable. Evidently, both types of bases can be derived from the juvenal of either. All bacula of adult *Phyllotis darwini wolffsohni* examined resemble those of the juvenals of either *P. osilae* or *P. darwini* (fig. 7). Of eight bacula of adult *P. darwini caprinus,* five are of the juvenal type as in *wolffsohni,* the remaining three are of the usual concave type characteristic of the baculum of *P. darwini.* The difference in size between juvenal and adult type bacula in adult *caprinus* is not related to the overall size of the animals themselves (Table 1).

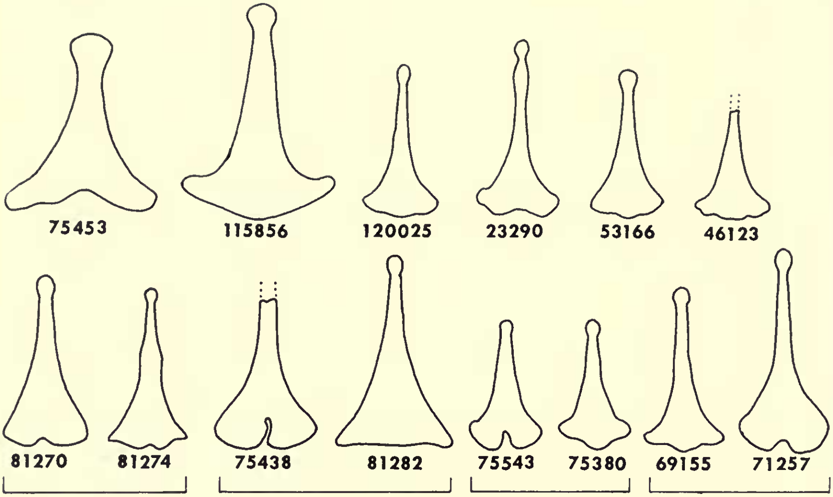

75453
115856
120025
23290
53166
46123
81270
81274
75438
81282
75543
75380
69155
71257

FIG. 6.—Bacula of phyllotines; distal digitate processes not shown.

EXPLANATION OF FIGURE 6

(5 digit numbers are of specimens in Chicago Natural History Museum, 6 digit numbers are of specimens in the Museum of Vertebrate Zoology, University of California.)

75453	*Phyllotis darwini* (Huancavelica, Huancavelica, Peru)
115856	" *osilae* (Pairumani, Puno, Peru)
120025	" *andium* (Matucana, Lima, Peru)
23290	" *micropus* (Río Inio, Chiloé Is., Chile)
53166	" *amicus* (Chosica, Lima, Peru)
46123	" *griseoflavus* (Belén, Catamarca, Argentina)
81270	" *gerbillus* (Piura, Piura, Peru)
81274	" " (Piura, Piura, Peru)
75438	" *pictus* (Tambo, San Miguel, Ayacucho, Peru)
81282	" " (Quilcayhuanca, Ancash, Peru)
75543	*Calomys sorellus* (Ocros, Ayacucho, Peru)
75380	" " " " "
71257	*Zygodontomys* (Muzo, Boyacá, Colombia)
69155	" (Socorré, Córdoba, Colombia)

A parallel relationship in size and shape of bacula exists between those of *Phyllotis osilae osilae* and *P. osilae phaeus*. The baculum of the first is comparable in size but not in shape to that of adult *P. darwini*. The single available baculum of an adult *P. o. phaeus* is juvenal in size and, though distinguishable from the baculum of sympatric specimens of *P. darwini*, can just as readily be assigned to *P. osilae* as to allopatric *P. darwini* on the basis of its shape (fig. 7).

The size and shape of the baculum in adult phyllotines varies locally and geographically (fig. 8, Table 1). The smallest baculum occurs in the large race *Phyllotis darwini wolffsohni*. The baculum of the largest race, *P. d. magister*, is no larger than that of the smallest race, *P. d. rupestris*. The difference in size of bacula of the Camataquí and Tilcara series of *P. d. caprinus* (fig. 7) is startling. That of the former is small and agrees with *wolffsohni*, while that of the latter is nearly as large as the baculum of *rupestris*. The Camargo and Tarija specimens show the same relationship, respectively. This accords with variation noted in the external, cranial and dental characters of *P. d. caprinus*.

Presence of thickenings or slightly developed processes on the mid-shaft region appears to be a local variable in *P. darwini*. The processes are present in all seven bacula of *P. darwini magister* which were examined and in the two preserved bones of the intergrading series of *P. d. posticalis* from Puquio, Peru (fig. 7). Thickenings of the mid-shaft region occur sporadically in *P. d. rupestris* but not in representatives of the populations with which *magister* is sympatric. Three of the four preserved bacula of *P. d. posticalis* from Limbani, Peru, are also thickened at mid-shaft but the single baculum of sympatric *P. osilae* is not. There is a very slight mid-shaft thickening in some bacula of *caprinus* but the shaft appears to be smooth and evenly tapered in *wolffsohni*.

There is no relationship between cyclical changes in size of testes and size of baculum in adult phyllotines.

A correlation between the size and form of the baculum or the phallus as a whole and the adaptation of the animal to its external environment is not evident. The penis is designed for the deposition of sperm in that part of the female genital tract where fertilization may proceed most effectively. Variations in the form and function of the female reproductive tract exert selective pressures on the male reproductive system. The penis that cannot insure delivery of sperm to egg cannot insure the survival of its kind.

EXPLANATION OF FIGURE 7

(Numbers are of specimens in the Museum of Vertebrate Zoology, University of California.)

Phyllotis osilae osilae

114702 Pairumani, Puno, Peru
114696 " " "
120163 León, Jujuy, Argentina

Phyllotis osilae phaeus

116177 Limbani, Puno, Peru

Phyllotis darwini rupestris

114684 Pairumani, Puno, Peru (compare with sympatric *P. osilae osilae* above)
115887 " " " (compare with *P. d. posticalis* at right and *P. d. magister* below).

Phyllotis darwini posticalis

115809 Puquio, Ayacucho, Peru (compare with *P. d. rupestris* at left and *P. d. magister* below).
120003 Ayacucho, Ayacucho, Peru (compare with *P. osilae phaeus* above).
116136 Limbani, Puno, Peru (compare with sympatric *P. osilae phaeus* above).

Phyllotis darwini magister

115874 Tarata, Tacna, Peru
115878 " " " (compare both samples with *P. d. rupestris* and *P. d. posticalis* above).

Phyllotis darwini wolffsohni

120196 Comarapa, Santa Cruz, Bolivia
120194 " " " "
(compare both samples with *P. d. caprinus* and *P. andium* below and *P. o. phaeus* above).

Phyllotis darwini caprinus

120204 Tilcara, Jujuy, Argentina
119975 Camargo, Chuquisaca, Bolivia
120208 Tilcara, Jujuy, Bolivia
120201 Tarija, Tarija, Bolivia (compare with *P. d. wolffsohni* and *P. osilae osilae* above).
120132 Camataquí, Tarija, Bolivia.

Phyllotis andium

120034 Surco, Lima, Peru
120037 " " "
120025 Matucana, Lima, Peru
(compare all samples with *P. osilae* above).

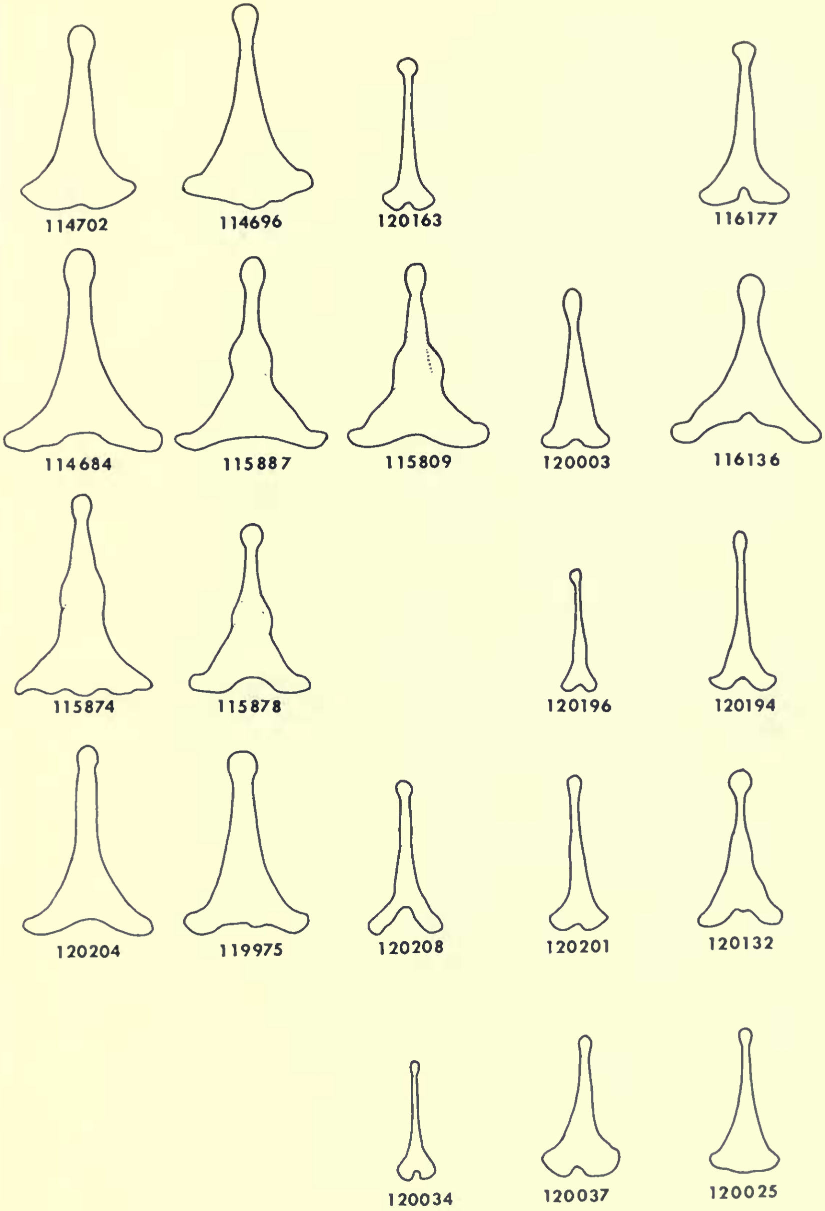

114702
114696
120163
116177
114684
115887
115809
120003
116136
115874
115878
120196
120194
120204
119975
120208
120201
120132
120034
120037
120025

FIG. 7.—Bacula of species and subspecies of the *Phyllotis darwini* complex; distal digitate processes not shown. See opposite page for explanation.

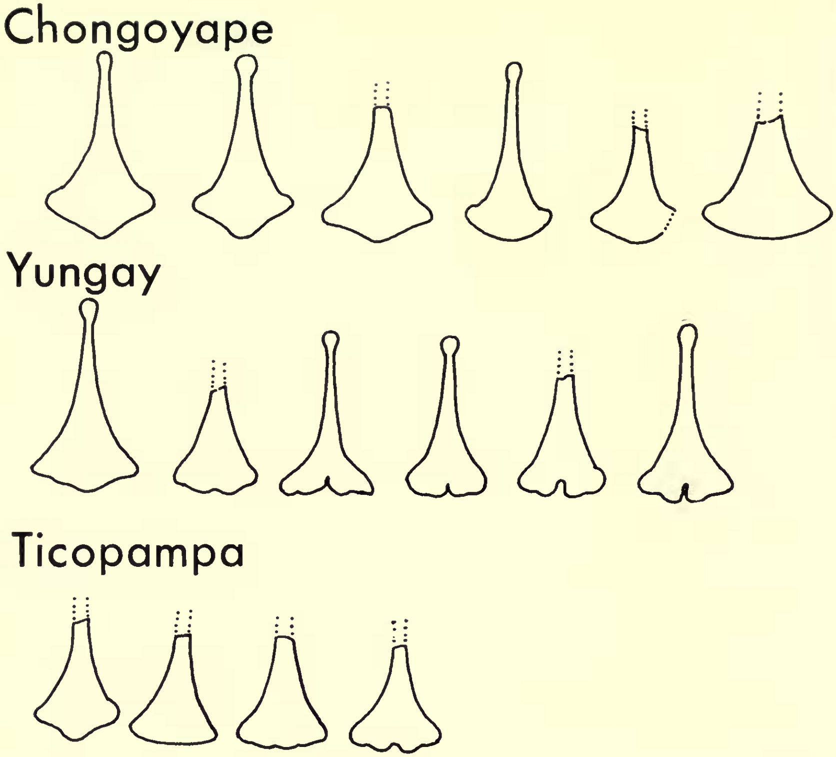


FIG. 8.—Bacula of *Phyllotis andium* showing individual and local variation; distal digitate processes not shown.

EXPLANATION OF FIGURE 8

(All bacula in Chicago Natural History Museum. Specimens shown from left to right are listed in order by their catalog numbers.)

81257	Chongoyape, Lambayeque, Peru
81255	” ” ”
81252	” ” ”
81253	” ” ”
81251	” ” ”
81256	” ” ”
81238	Yungay, Ancash, Peru
81247	” ” ”
81240	” ” ”
81243	” ” ”
81242	” ” ”
81246	” ” ”
81233	Ticopampa (Hacienda Catac), Ancash, Peru
81236	” ” ” ” ”
81232	” ” ” ” ”
81235	” ” ” ” ”

TABLE 1.—Individual and Geographic Variation in Size of Bacula in *Phyllotis* ssp.

Cat. No.	Locality	Baculum width and length	Testes length	Head and body length	Skull length	Weight of animal
Phyllotis darwini limatus						
114704	Atico, Arequipa, Peru	30 x 36	14	121	31.7	49
114705	Atico, Arequipa, Peru	28 x 34	6	112	29.4	38
116677	Atico, Arequipa, Peru	30 x 39	6	114	29.3	47
120062	Chosica, Lima, Peru	26 x 37	11	107	29.6	..
Phyllotis darwini posticalis						
120086	Casapalca, Lima, Peru	30 x 39	..	...	31.2	..
115809	Puquio, 15 km. NE., Ayacucho, Peru	29 x 38	12	134	33.2	72
116024	Puquio, 21 miles ENE., Ayacucho, Peru	30 x 42	12	128	33.2	64
120003	Ayacucho, Ayacucho, Peru	14 x 33	4	113	30.8	..
114679	Limbani, 8 miles SSW., Puno, Peru	30 x 40	12	127	32.9	70
114680	Limbani, 8 miles SSW., Puno, Peru	31 x 29	8	131	31.9	55
114683	Limbani, 8 miles SSW., Puno, Peru	32 x 39	13	125	32.8	75
116136	Limbani, 4 miles SSW., Puno, Peru	33 x 35	9	123	30.2	50
Phyllotis darwini magister						
115792	Rio Torata, 15 km. NE., Moquegua, Peru	19 x —	8	122	30.9	..
115874	Tarata, 1 km. N., Tacna, Peru	28 x 41	12	133	33.4	71
115877	Tarata, 1 km. N., Tacna, Peru	27 x 42	13	135	34.5	93
115878	Tarata, 2 km. N., Tacna, Peru	25 x 35	11	133	31.6	70
115879	Tarata, 2 km. N., Tacna, Peru	26 x 38	11	127	32.8	75
115881	Tarata, 4 km. N., Tacna, Peru	26 x 39	11	131	32.9	72
115883	Tarata, 4 km. N., Tacna, Peru	25 x 43	11	144	34.5	89
Phyllotis darwini rupestris						
115780	Arequipa, 7 km. E., Arequipa, Peru	26 x 32	9.5	105	28.8	40
115784	Arequipa, 7 km. E., Arequipa, Peru	21 x 32	7	88	27.3	25
115785	Arequipa, 7 km. E., Arequipa, Peru	22 x 31	8	96	27.2	26
115786	Arequipa, 12 km. SSW., Arequipa, Peru	27 x 36	9	104	29.2	..
115787	Arequipa, 12 km. SSW., Arequipa, Peru	23 x 36	10	102	29.2	..
116124	Arequipa, 52 miles ENE., Arequipa, Peru	28 x 37	..	110	29.5	48

TABLE 1.—Individual and Geographic Variation in Size of Bacula in *Phyllotis* ssp. (*continued*)

Cat. No.	Locality	Baculum width and length	Testes length	Head and body length	Skull length	Weight of animal
116126	Huaylarco, Arequipa, Peru	29 x 39	11	129	32.0	67
116127	Imata, Arequipa, Peru	26 x 36	12	120	30.3	50
116128	Salinas, Arequipa, Peru	29 x 41	. .	119	. . . .	49
114684	Pairumani, Puno, Peru	34 x 42	14	118	32.0	62
115887	Pairumani, Puno, Peru	31 x 40	13	121	31.1	63
114685	Santa Rosa, Puno, Peru	30 x 38	10	120	31.0	56
114686	Santa Rosa, Puno, Peru	25 x 34	12	105	29.3	44
115816	Ilave, Puno, Peru	28 x 40	12	114	30.7	54
115817	Ilave, Puno, Peru	34 x 39	12	107	31.4	53
115819	Juli, Puno, Peru	16 x 30	5	92	27.1	31
115822	Pampa de Ancomarca, Puno, Peru	26 x 32	11	110	28.5	46
115823	Pampa de Ancomarca, Puno, Peru	28 x 36	11	127	31.0	69
115825	Puno, 5 km. W., Puno, Peru	27 x 38	12	118	31.2	60
115888	Puno, 5 km. W., Puno, Peru	25 x 29	10	109	28.8	42
115827	Puno, 82 km. W., Puno, Peru	21 x 35	11.5	103	28.0	38
115891	Puno, 15 km. W., Puno, Peru	30 x 42	. .	126	32.8	68
115830	Río Santa Rosa, Puno, Peru	30 x 39	11	133	31.7	. .
115831	Río Santa Rosa, Puno, Peru	19 x 35	10	108	30.0	. .
115870	Pomata, Puno, Peru	27 x 40	11	119	31.2	64
116130	Asillo, Puno, Peru	27 x 38	11	118	30.2	46
116134	Tincopalca, Puno, Peru	— x 38	11	124	31.7	. .
116690	Juliaca, Puno, Peru	34 x 41	11	123	31.0	55
115799	Torata, 10 km. NE., Moquegua, Peru	25 x 36	9	97	28.5	40
115812	Lago Suche, Moquegua, Peru	26 x 34	11	111	31.7	61
115832	Tarata, 4 km. N., Tacna, Peru	28 x 36	11	123	31.6	. .
115837	Tarata, 4.5 km. N., Tacna, Peru	25 x 34	9.5	94	26.8	32
115838	Tarata, 4.5 km. N., Tacna, Peru	28 x 41	11	116	30.1	58
115840	Tarata, 2 km. N., Tacna, Peru	26 x 37	10	103	28.6	39
115843	Tarata, 2 km. N., Tacna, Peru	26 x —	8	99	27.7	35
115845	Tarata, 3 km. N., Tacna, Peru	28 x 38	9	101	30.0	39
115846	Tarata, 4 km. N., Tacna, Peru	27 x 37	10	113	29.5	52
115847	Tarata, 5 km. N., Tacna, Peru	— x 32	. .	94	28.2	32
115849	Tarata, 20 km. N., Tacna, Peru	25 x 36	12	112	30.4	56
115853	Tarata, 20 km. N., Tacna, Peru	26 x 35	10	111	31.5	52
116788	Tarata, 8 miles NE., Tacna, Peru	29 x 37	9 x 6	116	29.9	51
116792	Caritaya, Tarapacá, Chile	29 x 38	. .	110	29.9	43
116782	Caritaya, Tarapacá, Chile	26 x 37	10	114	29.1	50
116783	Caritaya, Tarapacá, Chile	28 x 32	10	104	. . . .	42
116784	Caritaya, Tarapacá, Chile	— x 36	10	117	. . . .	52
116778	Toconce, Antofagasta, Chile	30 x 37	8	113	29.5	50
116780	Toconce, Antofagasta, Chile	31 x 37	. .	118	28.3	43

TABLE 1.—Individual and Geographic Variation in Size of Bacula in *Phyllotis* ssp. (*continued*)

Cat. No.	Locality	Baculum width and length	Testes length	Head and body length	Skull length	Weight of animal
	Phyllotis darwini wolffsohni					
119978	Tapacari, Cochabamba, Bolivia	13 x 33	6	135	31.8	57
120183	Tapacari, Cochabamba, Bolivia	10 x 28	4	103	28.1	. .
120184	Tapacari, Cochabamba, Bolivia	10 x 27	4	117	30.8	52
120170	Punata, 8 miles NE., Cochabamba, Bolivia	10 x 29	4	114	29.0	49
120178	Punata, 10 miles NE., Cochabamba, Bolivia	8 x 27	4	112	29.4	42
120194	Comarapa, Santa Cruz, Bolivia	14 x 33	5	129	31.0	55
120196	Comarapa, Santa Cruz, Bolivia	7 x 25	6	116	30.5	52
	Phyllotis darwini caprinus					
120203	Tilcara, Jujuy, Argentina	24 x 37	10	116	30.4	
120204	Tilcara, Jujuy, Argentina	28 x 40	11	116	31.1	
120205	Tilcara, Jujuy, Argentina	26 x 38	11	123	32.2	
120208	Tilcara, Jujuy, Argentina	15 x 31	7	114	29.7	
119975	Camargo, Chuquisaca, Bolivia	26 x 38	7	122	30.7	47
120132	Camataquí, Tarija, Bolivia	17 x 32	7	118	31.4	56
120133	Camataquí, Tarija, Bolivia	11 x 23	4	116	28.1	35
120136	Camataquí, Tarija, Bolivia	12 x 23	4	101	29.0	39
120201	Tarija, Tarija, Bolivia	13 x 32	5	126	31.7	. .
	Phyllotis osilae osilae					
114691	Calacala, Puno, Peru	29 x 42	10	118	. . . .	51
114693	Calacala, Puno, Peru	33 x 44	10	125	28.2	55
114694	Calacala, Puno, Peru	29 x 39	12	124	30.8	53
114688	Calacala, Puno, Peru	29 x 43	7	124	30.8	55
114696	Pairumani, Puno, Peru	28 x 43	12	131	32.0	69
114702	Pairumani, Puno, Peru	24 x 38	9	105	27.6	32
114703	Pairumani, Puno, Peru	32 x 42	10	129	31.5	57
115855	Pairumani, Puno, Peru	29 x 43	11	124	31.9	66
115856	Pairumani, Puno, Peru	30 x 43	11	119	31.0	58
115857	Juli, Puno, Peru	27 x 38	10	122	31.4	70
115861	Puno, 15 km. W., Puno, Peru	26 x 37	12	120	30.7	51
115890	Puno, 5 km. W., Puno, Peru	30 x 37	10	116	31.3	52
115865	Pomata, Puno, Peru	25 x —	10	126	32.0	69
115866	Pomata, Puno, Peru	25 x 42	9.5	121	31.0	56
115867	Pomata, Puno, Peru	23 x 36	8	122	29.8	60
115868	Pomata, Puno, Peru	22 x 41	7	115	30.9	52
115869	Pomata, Puno, Peru	28 x —	9	127	31.1	62
115871	Pomata, Puno, Peru	23 x 38	8	118	30.6	47
116145	Asilla, Puno, Peru	24 x 40	7	115	30.4	.

TABLE 1.—Individual and Geographic Variation in Size of Bacula in *Phyllotis* ssp. (*continued*)

Cat. No.	Locality	Baculum width and length	Testes length	Head and body length	Skull length	Weight of animal
116686	Arapa, Puno, Peru	23 x 36	4	112	30.3	46
120163	León, Jujuy, Argentina	11 x 31	4	109	29.0	. .
116177	Limbani, Puno, Peru	19 x 32	6	126	31.5	54
Phyllotis andium						
120008	Canta, Lima, Peru	14 x 29	. .	100	27.5	. .
120017	Huaros, Lima, Peru	14 x 29	. .	103	28.8	. .
120022	Matucana, Lima, Peru	14 x 31	. .	106	28.0	. .
120023	Matucana, Lima, Peru	11 x 23	. .	95	26.6	. .
120024	Matucana, Lima, Peru	16 x 31	. .	103	27.8	. .
120025	Matucana, Lima, Peru	16 x 30	. .	111	29.3	. .
120034	Surco, Lima, Peru	9 x 25	. .	99	28.4	. .
120035	Surco, Lima, Peru	14 x 30	. .	105	28.4	. .
120037	Villavista, Lima, Peru	17 x 29	. .	116	30.5	. .
81232	Hacienda Catac, Ticopampa, Ancash, Peru	14 x —	. .	123	29.3	. .
81233	Hacienda Catac, Ticopampa, Ancash, Peru	14 x —	. .	111	27.7	. .
81235	Hacienda Catac, Ticopampa, Ancash, Peru	14 x —	. .	109	27.8	. .
81236	Hacienda Catac, Ticopampa, Ancash, Peru	14 x —	. .	110	27.3	. .
81238	Yungay, Ancash, Peru	17 x 29	. .	119	30.2	. .
81240	Yungay, Ancash, Peru	15 x 25	. .	97	27.5	. .
81247	Yungay, Ancash, Peru	13 x —	. .	113	28.2	. .
81243	Yungay, Ancash, Peru	12 x 24	. .	112	26.6	. .
81246	Yungay, Ancash, Peru	15 x 27	. .	117	28.3	. .
81242	Yungay, Ancash, Peru	14 x —	. .	117	28.5	. .
81251	Chongoyape, Lambayeque, Peru	13 x —	. .	99	26.4	. .
81252	Chongoyape, Lambayeque, Peru	17 x —	. .	99	26.7	. .
81253	Chongoyape, Lambayeque, Peru	14 x 26	. .	95	25.0	. .
81255	Chongoyape, Lambayeque, Peru	15 x 27	. .	103	25.7	. .
81256	Chongoyape, Lambayeque, Peru	20 x —	. .	114	27.6	. .
81257	Chongoyape, Lambayeque, Peru	17 x 29	. .	108	27.2	. .

DENTAL CHARACTERS AND EVOLUTION

Enamel Folds in Rodent Molar Evolution

The crown pattern of the molars of cricetines and many other rodents can be most accurately described in terms of the enamel folds. A name for each definable fold is as necessary a tool in the study of rodent phylogeny as a name for a primary cusp or loph. The fold terminology used here was proposed by me in 1944 (p. 14). Another very useful terminology based on beaver molars was devised by Stirton (1935, p. 392). However, the definitions of the folds as originally presented by these authors lack the precision and scope needed for present purposes. Enamel folds are now defined as fundamental dental features. It follows that all folds developed in the same way in the same place are homologous.

The letter symbols used in the following definitions are also shown in figure 9.

Major fold (MF): Based on posterior enamel wall, or ridge, of protocone(-id) and, except where enteroloph or ectolophid is well developed, continuous with anterior enamel ridge of the hypocone (-id). The major fold is the most convenient base reference for orientation and homologization of all quadritubercular molar elements.

First minor fold (NF 1): Based on posterior enamel ridge of anteroconule(-id) and continuous with anterior border of protocone(-id); non-existent in absence of anteroconule(-id).

Second minor fold (NF 2): Based on anterior enamel ridge of posteroconule(-id) and continuous with posterior border of hypocone(-id); present in a few cricetines (e.g., *Punomys;* third upper molar of *Neotomys*), in some murines and in many caviomorphs.

First primary fold (PF 1): Of upper molar, based on anterior enamel ridge of paracone and continuous with posterior border of anteroloph; may be obsolete or absent in molar with reduced or excessively worn procingulum. Of lower molar, based on posterior enamel ridge of metaconid and continuous with anterior ridge of either entoconid, or, if present, mesolophid.

Second primary fold (PF 2): First fold of tribosphenic, or primitive therian upper molar (Simpson, 1936), and most persistent through attrition and specialization; based on anterior ridge of metacone and continuous with posterior ridge of either paracone or, if present, mesoloph. Of lower molar, based on posterior ridge of entoconid and continuous with anterior ridge of posterolophid.

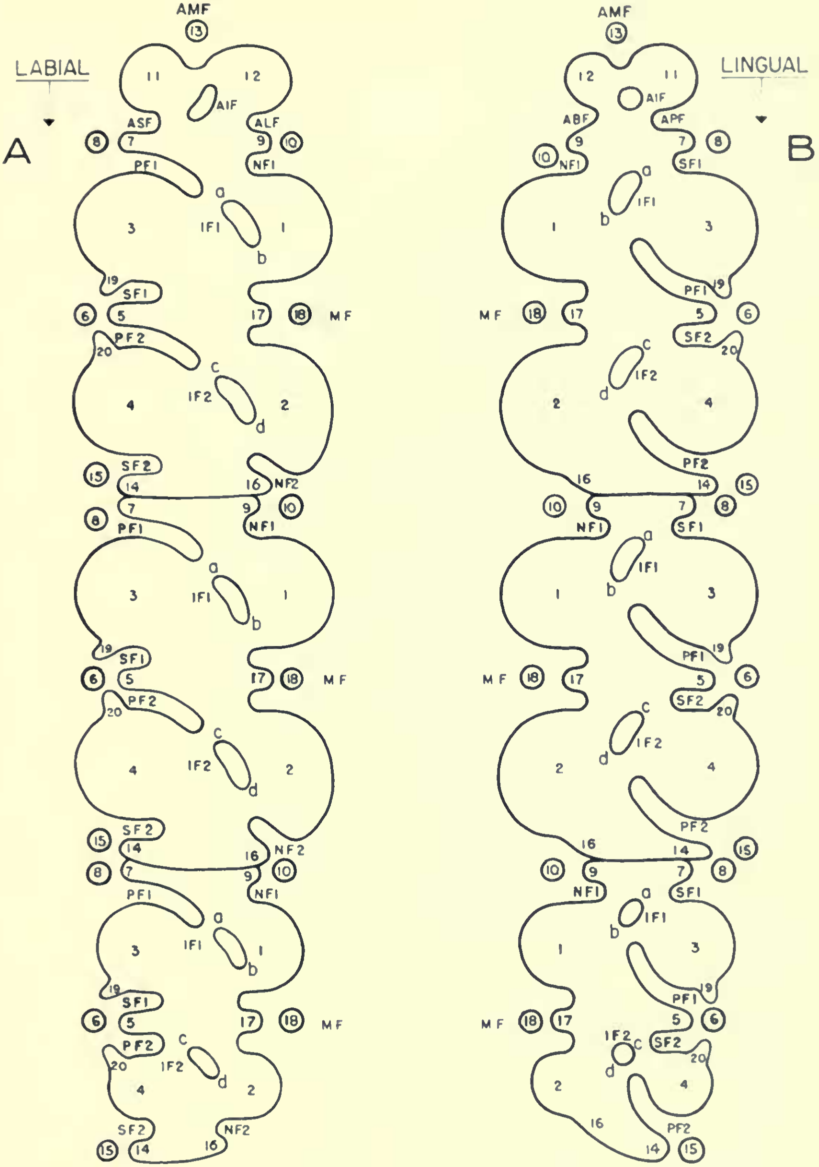
EXPLANATION OF FIGURE 9

NAMES OF FOLDS

MF	major fold
NF 1	first minor fold
NF 2	second minor fold
PF 1	first primary fold
PF 2	second primary fold
SF 1	first secondary fold
SF 2	second secondary fold
IF 1	first internal fold
IF 2	second internal fold
AIF	anterior internal fold
AMF	anterior median fold
ASF	anterior secondary fold (upper molars only)
ALF	anterior lingual fold (upper molars only)
ABF	anterior labial fold (lower molars only)
APF	anterior primary fold (lower molars only)

NAMES OF CUSPS

Upper Molars (A)		*Lower Molars* (B)
1. Protocone		1. Protoconid
2. Hypocone		2. Hypoconid
3. Paracone		3. Metaconid
4. Metacone		4. Entoconid
5. Mesoloph	mesolophostyle (-id)	5. Mesolophid
6. Mesostyle		6. Mesostylid
7. Anteroloph	Procingulum	7. Anterolophid
8. Anterolabial style		8. Anterolingual stylid
9. Anteroconule		9. Anteroconulid
10. Anterolingual style		10. Anterolabial stylid
11. Anterolabial conule		11. Anterolingual conulid
12. Anterolingual conule		12. Anterolabial conulid
13. Anteromedian style		13. Anteromedian stylid
14. Posteroloph	Postcingulum	14. Posterolophid
15. Posterostyle		15. Posterostylid
16. Posteroconule		16. Posteroconulid
17. Enteroloph		17. Ectolophid
18. Enterostyle		18. Ectostylid
19. Paralophule		19. Metalophulid
20. Metalophule		20. Entolophulid
a. Antero-median protolophule		a. Antero-median protolophulid
b. Postero-median ”		b. Postero-median ”
c. Antero-median hypolophule		c. Antero-median hypolophulid
d. Postero-median ”		d. Postero-median ”


LABIAL
A
AMF
13
11
12
AIF
ASF
ALF
8
7
9
10
PF1
NF1
a
3
IF1
1
b
19
SF1
6
5
17
18
MF
PF2
20
c
4
IF2
2
d
SF2
15
14
16
NF2
LINGUAL
B
AMF
13
12
11
AIF
ABF
APF
10
9
NF1
7
8
SF1
a
IF1
b
1
3
PF1
19
MF
18
17
5
6
SF2
20
c
IF2
d
2
4
PF2
16
14
15

UPPER RIGHT MOLARS LOWER LEFT MOLARS

FIG. 9.—Master plan of the occlusal surface of rodent molars showing all elements present in the enamel pattern of Muridae. Supernumerary lophules (-ids) present in the third molars of some forms (cf. *Otomys*, fig. 16, A) are not shown. For key to numbers and abbreviations see opposite page.

First secondary fold (SF 1): Of upper molar, based on anterior enamel ridge of mesoloph; sometimes divided into lateral and median portions by a paralophule; non-existent in absence of mesoloph. Of lower molar, based on posterior enamel ridge of anterolophid; non-existent in absence of anterolophid.

Second secondary fold (SF 2): Of upper molar, based on anterior border of posteroloph and continuous with posterior enamel ridge of metacone; non-existent in absence of posteroloph. Of lower molar, based on posterior enamel ridge of mesolophid; sometimes divided into lateral and median portions by an entolophulid; non-existent in absence of mesolophid.

First internal fold (IF 1): Enamel island defined by internal enamel ridges or lophules(-ids) connecting protocone(-id) with paracone (or metaconid); may be coalesced with first primary or first secondary fold.

Second internal fold (IF 2): Enamel island defined by internal enamel ridges or lophules(-ids) connecting hypocone(-id) with metacone (or entoconid); may be coalesced with second primary or second secondary fold.

In rodents with premolars absent, the procingulum of the first molar is hypertrophied and plicated. The resultant lophs and conules duplicate in appearance the structures immediately behind and partially replace the functions of the premolar lost in front. The folds defining the components of the procingulum are defined as follows:

Anterior median fold (AMF): Loop defining internal borders of anterolingual and anterolabial conules(-ids); may be weakly defined in the specialized molar or isolated and coalesced with anterior internal fold defined below.

Anterior secondary fold (ASF): Defines opposing enamel walls of anterolabial conule and anteroloph.

Anterior lingual fold (ALF): Defines opposing enamel walls of anterolingual conule and anteroconule.

Anterior primary fold (APF): Defines opposing enamel walls of anterolingual conulid and anterolophid.

Anterior labial fold (ABF): Defines opposing enamel walls of anteroconulid and anterolabial conulid.

Anterior internal fold (AIF): Enamel island defined by internal enamel ridges or lophules(-ids) connecting anterolingual and anterolabial conules(-ids); not to be confused with secondarily isolated anterior folds with which it may be coalesced.

Supernumerary folds: In some rodents, for example, *Otomys* (fig. 16, A), there is a tendency for the development of supernumerary crests posteriad to the posteroloph(-id) or posteroconule(-id) of the third molar. The folds defining these conules are treated as supernumerary secondary folds (SF 3, SF 4, etc.) or supernumerary minor folds (NF 3, NF 4, etc.).

Summary.—Folds based on the main cusps of the primitive therian molars are the *major* and the two *primary* folds. The *minor* and *secondary* folds are based on lophs and other secondarily developed dental elements. Folds based on homologous cusps and lophs are correspondingly homologous. Folds based on derivatives of the anterior cingulum of the first molar and of the posterior cingulum of the third molar are analogous or, rather, homoplastic structures. Simple accessory styles are not defined by folds, even when originating from or secondarily fused with, elements identified with folds.

The first fold to characterize the tribosphenic upper molar is the *second primary* (PF 2). The *major fold* (MF) is the second to appear in phylogeny. This fold delimits the hypocone and marks the quadritubercular upper molar. The first fold of the tribosphenic lower molar was one between paraconid and metaconid. In therians, such as rodents that have lost the paraconid, the *first primary* (PF1) and the *major fold* (MF) are the oldest. In the upper molar, the *first primary* and the two *secondary* folds delimit the lophs already present in the earliest cricetine molars. Internal and median folds appear last and are secondary modifications developed within the cricetine line. *Minor* folds inaugurate the cycle of specialization. The *second minor* fold, especially, is a development of the grazing type of molar in several rodent lines.

In lower molars *major* and *minor* folds may be regarded as equivalents of corresponding folds of the upper molars. *Primary* and *secondary* folds, on the other hand, are not equivalents of the same named folds of the upper molars. The same terminology is used, nevertheless, for convenience.

Once the maximum number of folds have become established in a species, their order of isolation and disappearance, whether through attrition in the individual or specialization in the line of descent, is the inverse of their order of appearance in phylogeny. Thus, the *second primary* fold, the first fold to define the tribosphenic upper molar, is the last to disappear.

Procingulum and Postcingulum

Homologies of the primary cusps and lophs of cricetine cheek teeth defined by Wood and Wilson (1936) have been generally accepted. However, attempts to apply extensively the Wood and Wilson definitions for derivatives of the cingulum meet with difficulties.

The cingulum of the quadritubercular molar in rodents is discontinuous. The anterior and posterior portions are most developed, and, in the more generalized tooth, they give rise to tubercles similar in form and structure to primary cusps and lophs. Lateral portions of the cingulum may appear in the form of well-defined ledge-like outgrowths supporting one or more stylar processes. These processes, however, may be present with only the merest trace of their original lateral cingular base.

The terms *anterior cingulum* and *posterior cingulum* have been applied not only to these basic portions of the cingulum but have been used at times for elements secondarily derived from the cingula. To avoid ambiguity, the terms *procingulum* and *postcingulum,* proposed by me in 1955 (p. 651), are reintroduced for the complex derived from the anterior cingulum and the complex derived from the posterior cingulum, respectively. These terms are particularly useful in the analysis of murid molars. They are defined as follows:

Procingulum, upper molars: Anterior cingulum with the following complex of functional elements derived from it:

(a) *Anteroloph* (fig. 9, A 7): Anteroloph of Wood and Wilson ("anterior cingulum" of some authors).

(b) *Anterolabial style* (fig. 9, A 8): When present usually fused with anteroloph; if not discrete, its presence indicated when combined elements extend to lateral margin of tooth.

(c) *Anteroconule* (fig. 9, A 9): Small anterior cone defined by first minor fold.

(d) *Anterolingual style* (fig. 9, A 10): When present never well developed and generally juxtaposed against anteroconule.

(e) *Anterolabial conule* (fig. 9, A 11): Always present in first molar with well-developed procingulum; absent as discrete element in second and third molars.

(f) *Anterolingual conule* (fig. 9, A 12): Like preceding, always present in first molar with well-developed procingulum; absent in second and third molars.

Note: *Anterolabial* and *anterolingual conules* may have been originally independent and discrete derivatives of the anterior cingulum, and the two may subsequently have fused into a single cone, the *anterocone* of Wood and Wilson. The possibility, however, that a simple anterocone is the primitive structure in rodents cannot be discounted.

(g) *Anteromedian style* (fig. 9, A 13): When present arising from anteromedian border of anterior cingulum; rarely well developed.

Postcingulum, upper molars: Posterior portion of cingulum with the following complex of functional elements derived from it:

(a) *Posteroloph* (fig. 9, A 14): Posteroloph of Wood and Wilson ("posterior cingulum" of some authors).

(b) *Posterostyle* (fig. 9, A 15): When present usually fused with posteroloph; if not discrete, presence indicated when combined elements extend to lateral margin of tooth.

(c) *Posteroconule* (fig. 9, A 16): Lateral posterior cone defined by second minor fold; analogous to anteroconule in origin.

(d) *Supernumerary crests:* See definition below (p. 76).

Procingulum, lower molars:

(a) *Anterolophid* (fig. 9, B 7): Less developed than anteroloph.

(b) *Anterolingual stylid* (fig. 9, B 8): Usually absent; when present less developed than corresponding element (anterolabial style) of upper molar.

(c) *Anteroconulid* (fig. 9, B 9): Frequently present when corresponding element (anteroconule) of upper molar is absent.

(d) *Anterolabial stylid* (fig. 9, B 10): Generally present in juxtaposition with anteroconulid and more developed than corresponding element (anterolingual style) of upper molar.

(e) *Anterolingual conulid* (fig. 9, B 11).

(f) *Anterolabial conulid* (fig. 9, B 12).

Note: Anterolingual and anterolabial conulids together compose the anteroconid of Wood and Wilson.

(g) *Anteromedian stylid* (fig. 9, B 13): Arising from anterior border of cingulum; rarely present.

Postcingulum, lower molars:

(a) *Posterolophid* (fig. 9, B 14), and *posterostylid* (fig. 9, B 15): When present, generally better developed than corresponding elements of upper molar. The *posteroconulid* (fig. 9, B 16) may be present or absent irrespective of presence of posteroconule.

(b) *Supernumerary crests:* See definition below.

Supernumerary crests, upper and lower molars:

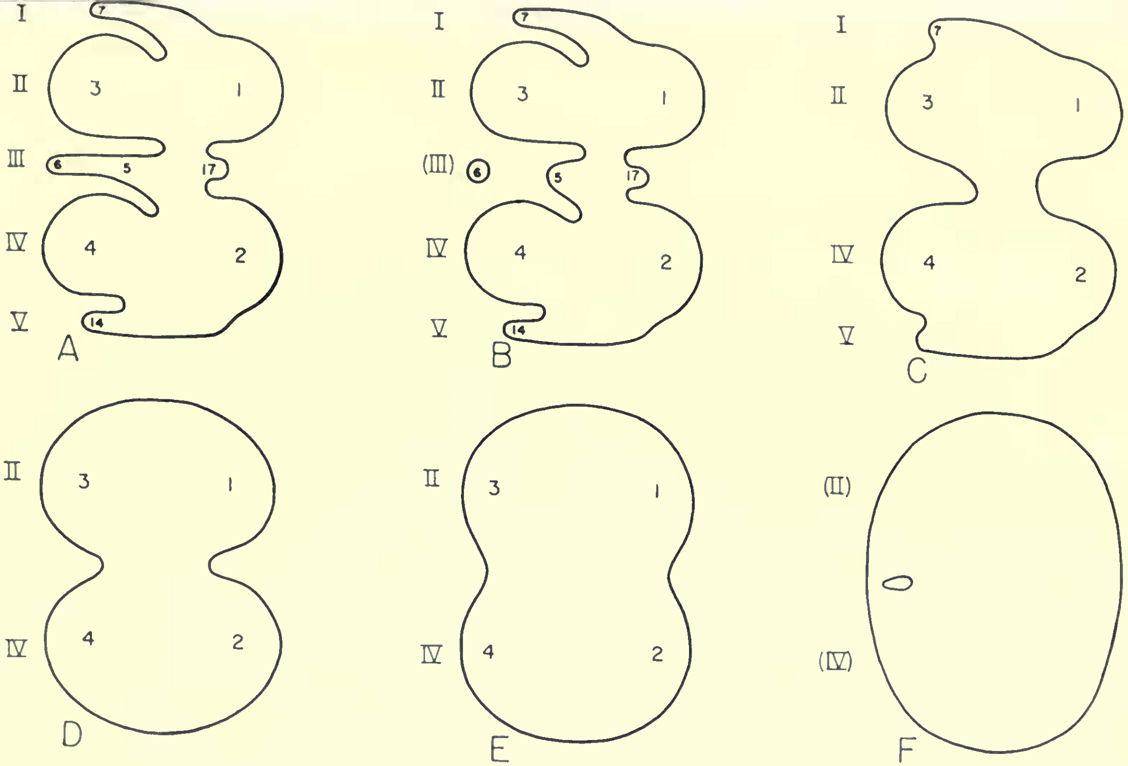
A crest, or series of crests, in the form of cuspules, lophs or laminas, may develop posteriad to the posteroloph(-id) or posteroconule(-id) of the third molar. Such supernumerary structures are absent in cricetines and murines but are present in otomyines (fig. 16, A), microtines and gymnuromyines (fig. 16, D). They are here classified as postero-supernumerary crests, lophs, or laminas. The folds defining them are a continuation of the numerical sequence of secondary folds and minor folds (see p. 73).

The Mesoloph in the Pentalophodont and Tetralophodont Patterns

Figure 10

The complex, or pentalophodont, cricetine molar is characterized by five primary transverse crests. Those of the upper molar are defined by I, procingulum; II, paracone; III, mesoloph fused with mesostyle; IV, metacone; V, postcingulum. The primary transverse crests of the lower molar are defined by I, procingulum; II, metaconid: III, mesolophid fused with mesostylid; IV, entoconid; V, postcingulum. The procingulum and postcingulum are described (see p. 74). All molars of oryzomyine, thomasomyine and some peromyscine rodents (see footnotes 1–3, p. 84) are pentalophodont.

The secondarily simplified, or *tetralophodont,* cricetine molar is marked by the same primary transverse crests that characterize the complex molar except that crest III, the fused mesoloph-mesostyle (-id) complex is disjunct, incomplete or absent. Derivatives of the tetralophodont molars are the *trilophodont* molar, with crest III and either crest I (procingulum) or crest V (postcingulum) obsolete or indefinable; the *bilophodont* molar, with crests I, III, and V obsolete or indefinable; and the *cylindriform* molar, with only crest II cer-


I
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III
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4
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A
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C
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2
D
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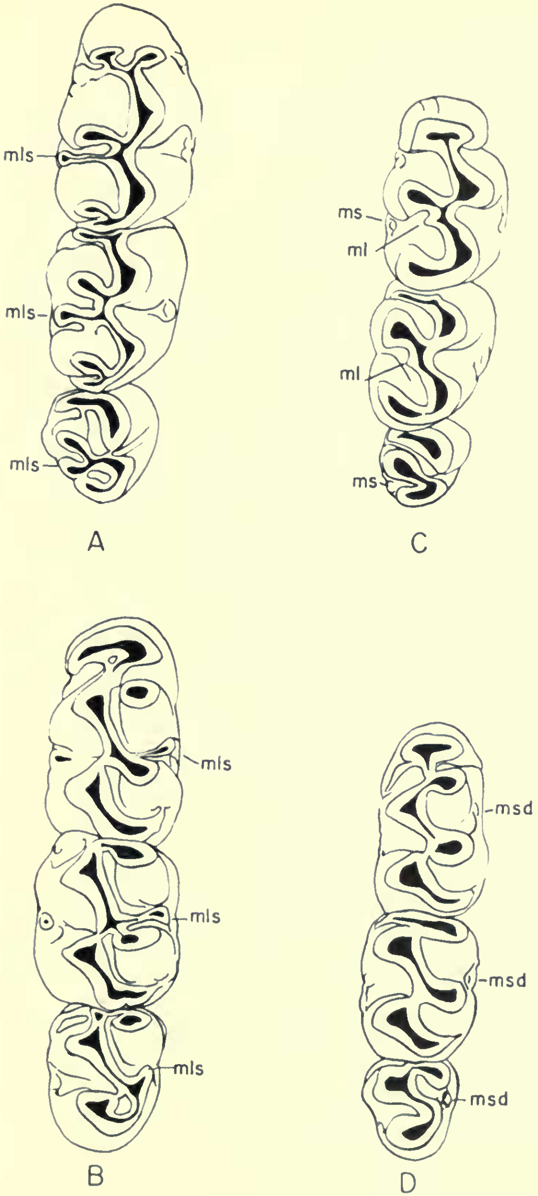
IV
3
1
4
2
E
(II)
(IV)
F

FIG. 10.—Evolution of the occlusal surface of a generalized cricetine molar from complex to simple (for names of folds, cusps, etc., see fig. 9). A, complex or pentalophodont molar showing the five-crested (I–V) pattern; B, simplified or tetralophodont molar with disjunct mesoloph-mesostyle (5 and 6); C, tetralophodont molar with transverse crests I and V obsolescent; D–F, further simplification of the tetralophodont molar from bilophodont to cylindriform patterns.

tainly definable. No sharp line can be drawn between the tetralophodont and derivative patterns. As a rule, even the cylindriform molar in the uneroded state retains signs of the erstwhile discreteness of one or more of crests I, IV, and V. Cricetines with basic tetralophodont patterns are all the New and Old World species except those of the groups mentioned in the preceding paragraph.

There is considerable variation in the degree of disjunction, reduction, or obsolescence, of crest III, in certain cricetines of the tetralophodont groups. Here, mesoloph(-id) and mesostyle(-id) are independent of each other. Either element may be present in the absence of the other, or both may be present in some molars and absent in others of the same specimen. In no case are mesoloph (-id) and mestostyle(-id) simultaneously present in all upper and lower molars. Hooper (1952, pp. 177–183) attempted to show that the dental pattern of the tetralophodont group, represented by *Reithrodontomys* (s.s.), graded into that of the pentalophodont group, represented by *Aporodon*. His observations were based on 2486 specimens of all species of the genera concerned. Hooper analyzed only the first and second upper molars and made no distinction between independent mesoloph and mesostyle and the same elements fused as a single functional element, the mesolophostyle. Examination of the same species in the collections of Chicago Natural History Museum and the University of Michigan Museum of Zoology reveals that in *Aporodon* a fused mesoloph-mesostyle is present in all upper molars and a fused mesolophid-mesostylid is present in all lower molars. On the other hand, in no species of *Reithrodontomys* (s.s.) are there either fused or independent mesoloph and mesostyle in the third upper molar, and in no species are there fused or independent mesolophid and mesostylid in any of the lower molars (fig. 11). In worn first and second upper molars of some specimens of *Reithrodontomys*, the crown surfaces of mesoloph and mesostyle may be abraded to the same level and appear to be a single continuous mesoloph–mesostyle. The unworn molars in the same species, however, reveal the mesoloph and mesostyle as truly discrete elements.

The evidence presented here, and, inadvertently, by Hooper (see fig. 11) shows no intergradation in dental characters between *Aporodon* and *Reithrodontomys*. The discrepancy seems to be slight but is highly significant in a group of intimately related forms where differences are more often relative than absolute, and where parallel development of similar but independently acquired characters is commonplace.


mls
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A
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FIG. 11.—A, B, right upper and left lower molars of *Aporodon tenuirostris*, showing well-developed mesoloph-mesostyle(-id) (*mls*); C, D, right upper and left lower molars of *Reithrodontomys fulvescens* with mesoloph (*ml*) obsolescent, mesolophid absent, and independent mesostyle (*ms*) and mesostylid (*msd*) present. Note the advanced stages of lamination in m^3 and sigmation in m_3. (After Hooper, 1952, figures 4C, D, 5C, D.)

The mesoloph(-id) arose in some groups of Rodentia before cricetines were defined. The mesostyle antedates the Rodentia. It is moot whether the ancestral cricetine molar was characterized by an independent mesoloph(-id) and mesostyle(-id) or by the fusion of the two elements. Either arrangement could have arisen independently and either could develop from the other. It is significant, however, that in living New World cricetines the fused mesoloph–mesostyle(-id) occurs only in the more generalized molars. With specialization, mesoloph(-id) and mesostyle(-id) degenerate, lose their triturative function and become obsolete or disappear altogether in hypsodont, laminate, triangulate and all other advanced types of cricetine molars. On the other hand, some Old World murids, such as the Malagasy *Gymnuromys* (fig. 16, D), have retained the fused mesoloph–mesostyle(-id) through the processes described below (pp. 86–93) as planation, hypsodonty and advancing lamination. In another phyletic line, represented by *Neocometes* Schaub and Zapke (fig. 16, C) of the European Miocene, the fused mesoloph–mesostyle(-id) persisted through stages of planation and lamination.

The "Pseudomesoloph" and the Dental Pattern in Cricetine Systematics

In some cricetines a "pseudomesoloph(-id)" (fig. 12) appears in one or more molars, most commonly the first or second upper and the first lower. This false "mesoloph" is the paralophule (fig. 9), an enamel extrusion of the posterior border of the paracone. The false "mesolophid" is the entolophulid (fig. 9), which originates from the anterior border of the entoconid. In contrast, the true mesoloph(-id) is derived from the longitudinal enamel ridge (the mure, or Längsgrat) connecting protocone with hypocone (protoconid with hypoconid). In many species lophule(-id) and mesoloph(id) are present in the same tooth as discrete elements. In cricetines such as the phyllotine *Zygodontomys*, without mesoloph(-id), the "pseudomesoloph," i.e., the paralophule, is sometimes well developed. Its linkage with the mesostyle adds to its simulation of the true mesoloph. Hoffmeister (1951, p. 14, fig. 7) described and figured a "pseudomesolophid" (i.e., entolophulid) in $m_{\overline{1}}$ of *Peromyscus truei* Shufeldt. Although he labeled and treated the element as a "mesolophid," Hoffmeister clearly distinguished (in text) this structure from the true mesoloph present in the upper molars of the same animal.

Some time after the manuscript of this paper was completed and submitted for publication, Hooper's (1957) remarkably detailed study of the accessory elements of the molars of the cricetine genus *Peromyscus* (sensu lato) came to hand. Unfortunately this work fails to distinguish paralophule and entolophulid from mesoloph and mesolophid, respectively. Thus, some of the 8 diagrams presented by Hooper (op. cit., fig. 1, p. 9) to show the relationship between what are termed mesoloph(-id) and mesostyle(-id), require other interpretations. The first diagram (with caption "+") shows mesostyle(-id) free, as described. On the other hand, the succeeding diagrams, labeled 1 to 5 inclusive, show mesostyle and mesostylid fused with paralophule and entolophulid, respectively, not mesoloph or mesolophid, as implied in the caption and text. The ridge with which the mesostyle(-id) is coalesced in diagram 6 may be the true mesoloph(-id). The correct identification of that element can be determined only in the real tooth. The transverse ridge in diagram 7 is rightly identified as the mesoloph(-id) fused with the mesostyle(-id).

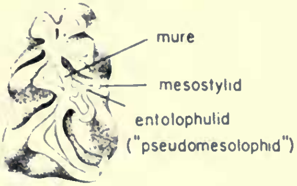

FIG. 12.—Left lower first molar of *Peromyscus truei gilberti* (after Hoffmeister, 1951, p. 14, fig. 7). The mure (or Längsgrat) is the median longitudinal enamel ridge connecting metaconid with entoconid. The true mesolophid (absent) is a diverticulum of the mure. The "pseudomesolophid" is the entolophulid, a ridge protruding from the entoconid. (For names of all parts of the tooth see fig. 9, p. 71.)

Bader (1959, p. 600) used Hooper's system for a statistical analysis of the dental traits in three species of Florida *Peromyscus*. Although he recognized that the true mesoloph(-id) and pseudomesoloph(-id) are not homologous, Bader treated them as one in computing their percentage of penetrance in each of the first two upper and lower molars.

Misidentification or confusion of paralophule and entolophulid with mesoloph and mesolophid, respectively, may lead to a misconstruction of the roles played by each of these elements in the evolutionary process. Paralophule and entolophulid are specializations that evolve *after* the mesoloph and mesolophid have become established. They may also originate while the mesoloph and mesolophid are becoming obsolete or have disappeared altogether. In the first instance, paralophule and entolophulid behave as accessories of the mesoloph and mesolophid, respectively. In the second instance, they act as functional replacements, i.e., as "pseudomesoloph" and "pseudomesolophid," respectively.

The metalophule and metalophulid (fig. 9) are analogous elements that may also be confused with the mesoloph and mesolophid, respectively. They are of infrequent occurrence and of no concern in the present discussion.

Regardless of the identifications made or the terminologies used, Hooper's statistical analyses, figures and graphs clearly reveal the precise styles(-ids), lophs(-ids), and lophules(-ids) involved in the enamel pattern of each of the 17 species of *Peromyscus* studied. The accumulated data prove that in all populations of some species of *Peromyscus* molar patterns are essentially stable. In other species, the patterns are geographically variable. Where such variability exists, Hooper (op. cit., p. 48) points out that "populations that inhabit arid situations . . . have simpler teeth, with fewer and smaller styles and lophs, than populations of the same species that live in denser cover in more humid areas. This is in harmony with a current hypothesis, namely that the mesoloph(-id) is vestigial or absent in molars of cricetines inhabiting open country and scrubland. (Hershkovitz, 1955: 644.)" Actually, the phenomenon exemplifies more than a hypothesis. It is a demonstration of a basic principle in cricetine evolution.

Variability in the dental pattern of some species led Hooper (op. cit., p. 53) to the conclusion that extraordinary reliance cannot be placed on accessory lophs and styles in the systematic analysis of the genus *Peromyscus*. No one would quarrel with this opinion. It is necessary to emphasize, however, that *Peromyscus*, as currently constituted, is unique among cricetines in containing some species which are ecologically and morphologically transitional between sylvan and pastoral groups. No question arises regarding the validity of dental characters in the systematics of species and genera whose evolution from sylvan to pastoral forms is no longer marked by contemporary annectants.

Dynamics of Rodent Molar Evolution

Dental modifications in the phylogenetic line leading to rodents were associated with hypertrophy of the incisor pair accompanied by a progressive decrease in number of teeth and a compensatory increase in the functional area and efficiency of the cutting, crushing, or grinding surfaces of the remaining cheek teeth. Loss of the primitive first and third incisors was adequately compensated by development of ever-growing median incisors that maintain virtually permanent cutting surfaces on an even and efficient operating plane. Loss of the first two premolars, and suppression, or reduction in number or size, of the last two, may be attributable in part to the increasing demands for calcium and alveolar space by the middle incisors and in part to the usurpation of their functions by those teeth. In many rodents, additional specializations of the incisors as seizers, diggers or triturators are correlated with simplification and reduction in number of the true molars. In extreme examples, the molars may degenerate into simple tools that serve merely for gripping food, or for mixing and blending with saliva the food already adequately comminuted by the incisors.

With establishment of the definitive rodent dental formulae, earliest molar modifications leading to the generalized pattern in cricetines and other rodent groups was accomplished by the process of *plication*, described below. Subsequent changes in molar structure have been effected by forces acting on the vertical and horizontal planes of the teeth. The processes described in the following as *planation* and *hypsodonty* operate in opposing directions of the vertical axis of the molar. *Lamination, involution, triangulation* and *fusion* model the molar in a horizontal sense. The first three horizontal forces are progressive and result in secondary *complications.* The fourth horizontal force, *fusion*, is retrogressive and results in secondary *simplifications* of the generalized plicident pattern. All processes involved are determined by inherent factors controlling growth and development. They operate in a definite direction throughout the evolution of the organism.

Plication

Plication, or infolding, of the enamel covering of the primitive upper brachyodont cheek tooth defines the *hypocone, procingulum, postcingulum*, connecting ridges between the main tubercles, certain *styles*, and a *mesoloph* (cf. pp. 76–80; fig. 10, A). The mesoloph, when present, develops from the *longitudinal ridge* (mure of Wood and Wilson, 1936; Längsgrat of Schaub, 1925) connecting the protocone and the hypocone and extends transversely nearly or quite to the outer border of the molar. Plication of the lower cheek tooth originates similar topographic features. The additaments of plication enumerated above result in a complex crown pattern of 5 transverse ridges (anticlines of Stehlin and Schaub, 1951, p. 30) separated by 4 valleys (synclines of Stehlin and Schaub, loc. cit.) opening on the outer side of the upper tooth and the inner side of the lower. The oldest known rodent with the complex plicident or *pentalophodont* molar pattern is the late Eocene *Theridomys* Jourdain (fig. 13) of Europe. Here the middle transverse ridge of the molar is the mesoloph fused with the mesostyle. Early cricetines such as *Eumys, Schaubeumys, Cricetodon, Heterocricetodon,* etc., show the mesoloph and mesostyle as either fused or independent structures. The same basic pattern, with slight modifications, has been acquired, probably independently, in the upper molars of the more generalized representatives of Castoridae, Eutypomyidae, Eomyidae, etc. (cf. Wood, 1947; 1955, pp. 165–185).

Recent American cricetines with complex plicident molars typified by the fused mesoloph and mesostyle include the species of oryzomyine[1], thomasomyine[2] and some peromyscine[3] rodents (figs. 4, A; 10, A; 11, A, B). These mice are primarily forest-dwellers. In deforested country they may survive in wooded ravines, shrub-covered cliffs and along brush-lined streams. They feed on herbaceous plants, pulpy fruits, soft seeds, fungi, and invertebrates. Grains do not constitute a significant part of the normal diet of woodland-inhabiting mice. Except for minor exceptions, it is unlikely that their diet and feeding habits have changed appreciably through geologic time. Adaptive radiation among these mice has affected external characters most, dental structure least. Known fossils of early Tertiary rodents of Europe and North America currently classified as cricetines are not ancestral to present forms. Most of them are more specialized dentally, but they may be offshoots of the same basic forest-inhabiting stock that has persisted without important modifications to this day.

A second division of cricetines with plicident molars consists of nearly all remaining forms, including the phyllotines of this monograph, sigmodonts, akodonts and pastoral peromyscines (*Podomys,*

[1] Composed of *Oryzomys* (subgenera: *Microryzomys, Oecomys, Melanomys, Nesoryzomys*), *Neacomys, Scolomys, Nectomys* (s.g., *Sigmodontomys*), *Megalomys*. For characters see Hershkovitz (1944, pp. 12–13).

[2] *Thomasomys* (synonyms: *Aepeomys, Inomys, Delomys, Erioryzomys, Wilfredomys*), *Phaenomys, Nyctomys, Otonyctomys, Rhipidomys*. The "*Acodon*" *dorsalis* Hensel, of Schaub (1925, p. 89, pl. 5, figs. 8, 10), the molars of which were carefully described by him as typical of the present group, is a species of *Thomasomys*.

[3] *Peromyscus* (*Peromyscus*, s.s. [part]; *Ochrotomys*, s.g.; *Megadontomys*, s.g.).

Haplomylomys, Onychomys, Baiomys, Reithrodontomys [s. s.], *Neotomodon, Scotinomys, Nelsonia, Neotoma, Xenomys, Ototylomys* and *Tylomys*). Their molars are characterized by all topographic features of the primitive plicident tooth, except that the mesoloph (and mesolophid) is never locked with the mesostyle (and mesostylid) in the unworn tooth; the mesoloph(id) is either reduced or absent in m^{1-3}, vestigial or absent in m_{1-2}, and absent in m_3. Thus, the unmodified crown pattern of the upper molar normally consists of 4 complete transverse ridges and 3 valleys opening on the labial border. The mesoloph sometimes present in m^{1-2} may be sufficiently developed to appear as an incomplete middle or "5th" crest (fig. 10, B). An occasionally present "pseudomesoloph"(-id) in the form of either a thickened mesostyle or an enamel evagination from the posterior border of the paracone (or from the anterior border of the entoconid) does not affect the basic crown pattern (fig. 12). According to Schaub (1925, p. 91) and Stehlin and Schaub (1951, pp. 169, 324, and elsewhere in the text), the simplified or *tetralophodont* cricetine molar differentiated from the complex, or pentalophodont, molar by regressive loss of the true mesoloph. This view is certainly correct. It is evidenced by the progressive simplification

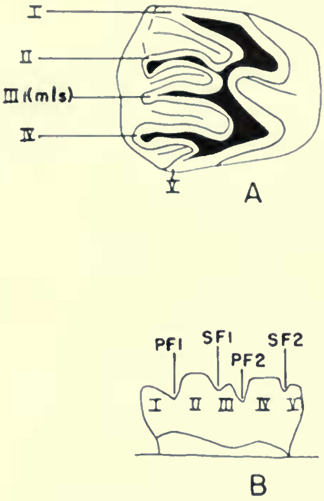

FIG. 13.—Primitive pentalophodont molar plan in *Theridomys* (European Eocene; after Stehlin and Schaub, 1951, fig. 23): A, upper right second molar; B, buccal aspect of same. For explanation of symbols see figures 9 and 10; *mls*=fused mesoloph and mesostyle.

of the molar to the trilophodont, bilophodont and cylindriform patterns (fig. 10), by analogy with other regressive elements in the molars of living cricetines and all other mammals, and, most convincingly, by ontogeny. The American fossil record is poor. There is a predominance of specialized pastoral forms, which are uncritically classified. Nevertheless, it does not contradict the present concept of phylogenetic sequence. The possibility that cricetines with simplified molars are collateral offshoots from a common ancestor with plicident molars in the premesoloph stage of development, can be discounted. The rudiment of a mesoloph, often present in tetralophodont molars of cricetines, is a vestige *derived from,* and not an emergent structure *leading to,* the pentalophodont molar pattern. The fused mesoloph-mesostyle(-id) is present only in bunodont, brachyodont molars. It may also be absent in such molars but it is never present in the specialized, hypsodont molars of cricetines.

Living cricetines with the simplified molar pattern are primarily pastoral, i.e., inhabitants of deserts, tundras, punas, savannas, scrublands and coniferous forests. Sometimes they occur as intrusive elements in bogs, meadows, or rocky situations within deciduous forests. A few aquatic species have survived in riverine habitats subsequently surrounded by climax forests; others may have invaded streams with banks deforested by man. The vast majority of pastoral species are ground-nesting, but many are good climbers and some have become semi-arboreal. A few species are aquatic. All feed mainly on grasses, lichens, mosses and grains. Some include pine needles and bark; others add insects, worms and small fish to the diet. The impact of this food, especially of harsh or siliceous grasses, on the molars, is considerably greater than that of the diet of forest-dwelling species with pentalophodont molars. The natural selective effects of the different feeding habits may account for the initial differentiation and subsequent radiation of the simplified, or tetralophodont, molar pattern.

The six processes of molar evolution described below have acted on the tetralophodont cheek tooth. Only the first process, planation, has had a moderate effect on the complex pentalophodont molar of some American cricetines.

Planation

Figures 14, 49

Once a complicated system of dental peaks, ridges and valleys has been developed, the process of planation may set in. As a rule,

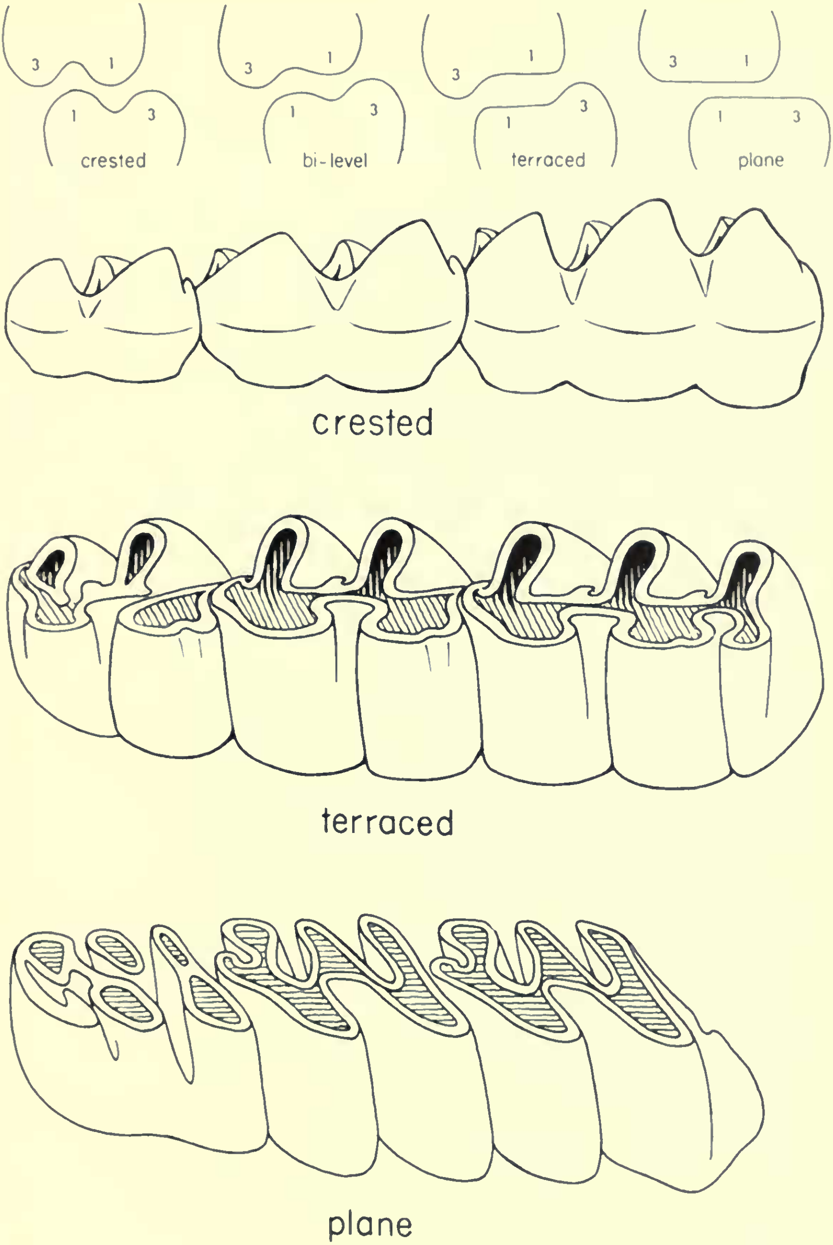
3
1
1
3
crested
3
1
1
3
bi-level
3
1
1
3
terraced
3
1
1
3
plane
crested
terraced
plane

FIG. 14.—Molar planation: evolutionary stages from primitive crested to specialized plane shown in front views of molars (upper row) and side views of molar rows. 1=protocone(-id); 3=paracone in upper, metaconid in lower (after Hershkovitz, 1955:649).

it advances simultaneously with hypsodonty. In either primitive (i.e., complex) or simplified molar types, early stages of planation are bilaterally unequal. Here the inner side of the upper molars and the outer side of the lower rise less rapidly. The *terraced* molar (fig. 14) that results is a recognizable and phylogenetically important stage in the succession of dental topography. In many species with plane molars, a terraced condition may persist in the newly erupted but unworn molars of juvenals. As a rule, the upper molars are in a more advanced stage of planation than the lower, and the third molar is more advanced than the other molars of the same jaw.

The pentalophodont pattern in living New World cricetines tends to retain its primitive bunodonty. Nevertheless, planation has progressed as far as the *terraced* stage in a number of oryzomyine and thomasomyine species.[1] On the other hand, the tetralophodont molars of New World cricetines show all stages of planation from the fully bunodont, or the crested, through the terraced to the completely plane. Examples of complete planation in molars of non-cricetine rodents with or without mesolophs, and in other orders of mammals, are too well known to require citation.

Hypsodonty

Figure 15

Hypsodonty is the evolutionary process that provides a longer wearing surface by an increase in the depth of the tooth. It is a rejuvenating process that counterbalances the effects of planation on teeth exposed to excessive attrition. Hypsodonty may result in either an elongate or a prismatic crown or in hypertrophy of the main tubercle or tubercles of the crown. These effects of hypsodonty may be described in two categories, as follows:

1. *Coronal hypsodonty: Vertical elongation of the entire crown of the tooth at the expense of the root.* This kind of hypsodonty is found only in molariform teeth specialized for crushing and grinding. It is typically present in grazing animals. New World cricetines with the primitive pentalophodont type of molars are forest-dwellers and, in the main, non-grazers. Coronal hypsodonty among them is absent or, at most, incipient. The quasi-pentalophodont molars of the Chinese hamster *Cansumys*, however, are not only hypsodont but selenodont as well, an exceptional tooth form in cricetines. The degree of

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[1] In the Malagasy murid *Gymnuromys* (fig. 16, D) specialization of the pentalophodont molar has reached the wholly plane condition.

hypsodonty in cricetines with the simplified or basic tetralophodont molar pattern reflects the extent to which each species has become adapted to the diet of savanna and scrubland vegetation. In most phyllotine rodents, the molar crowns are slightly to moderately hypsodont. The condition is more pronounced in sigmodonts and neotomines. Among murids in general, maximum development of coronal hypsodonty at the expense of the roots has been attained by microtines. Caviomorphs offer additional examples of molar crown hypsodonty. The classic example of coronal hypsodonty is the prismatic molar of the modern equine.

2. *Tubercular hypsodonty: Elongation of the coronal tubercle, or tubercles, at the expense of the remainder of the tooth, including the root.* This type of hypsodonty is an adaptation for seizing, grappling, stabbing, cutting, chopping or cracking. It may appear in any kind of tooth. The middle incisor of all rodents is an example of tubercular hypsodonty. The chisel-shaped tooth has developed in depth at the expense of its own root and the erstwhile root-encasing alveoli of the lost incisors, the canines and one or more of the premolars. The elephant tusk is another notable example of tubercular hypsodonty of the incisor. Canine teeth of many mammals are also hypsodont tubercles, but the root has persisted in most.

Tubercular hypsodonty of the molariform teeth is well developed in many marsupials, insectivores and insectivorous bats. It is also present in some cricetines, particularly the insect-eating *Onychomys* and in the fish-eaters *Rheomys, Ichthyomys,* etc. Here, the molar cusps have developed into prong-like projections for seizing and cracking elusive, hard-coated, mobile prey. The spiked cusps of the insect- and fish-eating rodents are quickly eroded but not before the peculiar seizing and chewing patterns have become established. In the central African murid *Deomys* (Deomyinae) the molar tubercles are notably elongated and those of both sides of the upper molars are hooked backward. Evidently, the primary function of the molars of *Deomys* (fig. 15, B) is the grappling and chopping of such wiggling, soft-bodied prey as earthworms and caterpillars. The molars appear to be of little value as crushers and grinders even when worn.

The history of hypsodonty and its correlation with the type and mineral content of plants eaten by herbivorous mammals has been reviewed by White (1959, p. 211). This author defines three kinds of molar hypsodonty. Type 1, called *cusp hypsodonty,* corresponds roughly to my coronal hypsodonty. I do not, however,

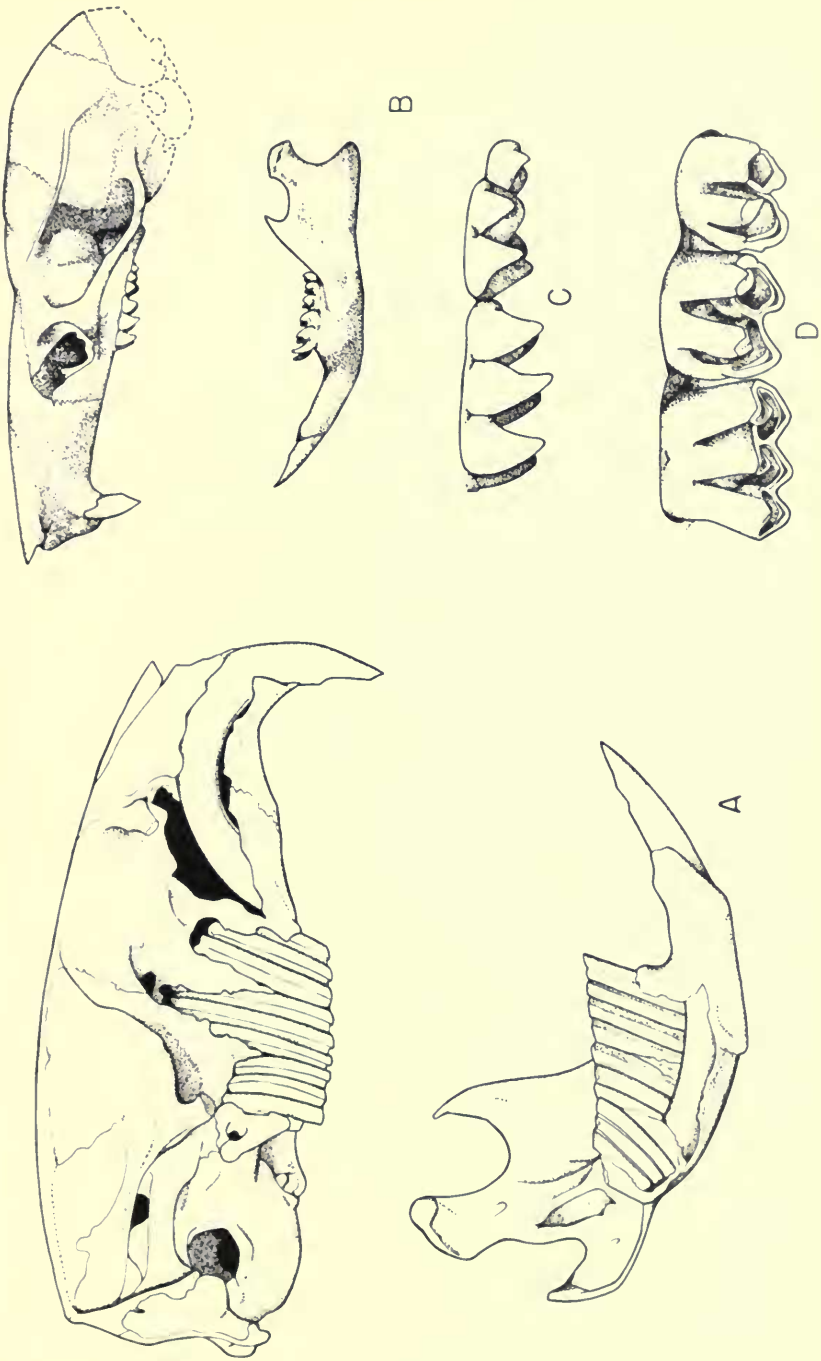
FIG. 15.—Hypsodonty in murid rodents.

A. Coronal hypsodonty of molars and tubercular hypsodonty of incisors shown in a dissected side view of the skull and left mandible of the European microtine *Arvicola amphibius* Linnaeus (after Hinton, 1926, fig. 12).

B. Tubercular hypsodonty shown in side view of skull and left mandible of the African murid (Deomyinae), *Deomys ferrugineus* Thomas.

C. Tubercular hypsodonty shown in buccal view of left upper molars of *Deomys ferrugineus*.

D. Seleno-hypsodonty, a combination of tubercular hypsodonty (on buccal side shown) and coronal hypsodonty (on lingual side), exhibited in three-quarter view of left upper molars of the Chinese cricetine, *Cansumys canus* G. M. Allen.


A
B
C
D

regard the Suidae, included by White in type 1, as a family characterized by hypsodont molars irrespective of some individual exceptions. White's type 2, *tooth-base hypsodonty,* should, by definition, exclude anything assigned to type 1. It seems to me, however, that molars of most of the taxons included in type 2 can just as well be referred to type 1, while others, as suggested by White, can be treated as intermediate between types 1 and 2 or made subjects of a separate category. Type 3, named *root hypsodonty,* includes animals with molars which, in my opinion, can be indifferently referred to either type 1 or 2, and molars of other animals which are rootless according to all authorities, including White. Elsewhere, White (cf. p. 260) equates hypsodonty with "high crowned" only.

Whatever species or genera he may have had in mind in erecting the three types of hypsodonty, White cites only supergeneric taxons, mostly families and orders, as products of each type. He feels (p. 261) that not enough is known of the larger groupings of hypsodont mammals to permit a satisfactory categorization of the lower taxonomic grades. In the present discussion, however, I prefer to regard hypsodont teeth as parts of specific animals. Such teeth can be classified by any convenient standard which serves to illustrate the effects of hypsodonty on their form and function.

Lamination

Figures 16, 17

Lamination is the process of transection of a molar crown by confluence of a fold of one side of the tooth with another of the opposite side. The lamina formed is composed of one or more elements (cusp, conule, loph or "lophostyle") of one side of the tooth combined with at least one analogous element of the opposite side of the tooth.

Lamina are classified according to their orientation relative to the antero-posterior axis of the molar.

1. *Transverse:* Formed by confluence of opposing, transversely directed folds. Transverse folds are common among rodents in general. They are present in the simplified, or tetralophodont, pattern of some living cricetines, including phyllotines with unworn or slightly worn molars (fig. 44, *c* [$\mathrm{m}^{\underline{2}}$], fig. 69, *e* [$\mathrm{m}_{\overline{1}}$]), but are absent in the pentalophodont molars of New World cricetines. However, they occur in a highly specialized group of the European Miocene represented by *Neocometes* Schaub and Zapfe (fig. 16 C).

2. *Oblique:* Formed (a) by confluence of a fold of one side with either the anterior or posterior alternating fold of the opposite side, or (b) as a transverse lamina but with the entire molar rotated approximately 20° to 90°. Oblique lamina are present in the molars of many caviomorphs and other rodents, including some living species of tetralophodont cricetines (fig. 68, *c* [$m^{\underline{3}}$]).

3. *Chevron:* Formed by confluence of obliquely directed opposing folds. These folds are present in some caviomorphs and murines but are absent in cricetines.

The figure 8 pattern in simplified tetralophodont molars of many cricetines is a condition of incomplete transverse lamination between opposite folds. The same design may also occur as a residue in laminated molars worn to the base of the folds.

Subdivision of a lamina into its original components may be effected by the processes of *involution* and *triangulation,* defined below.

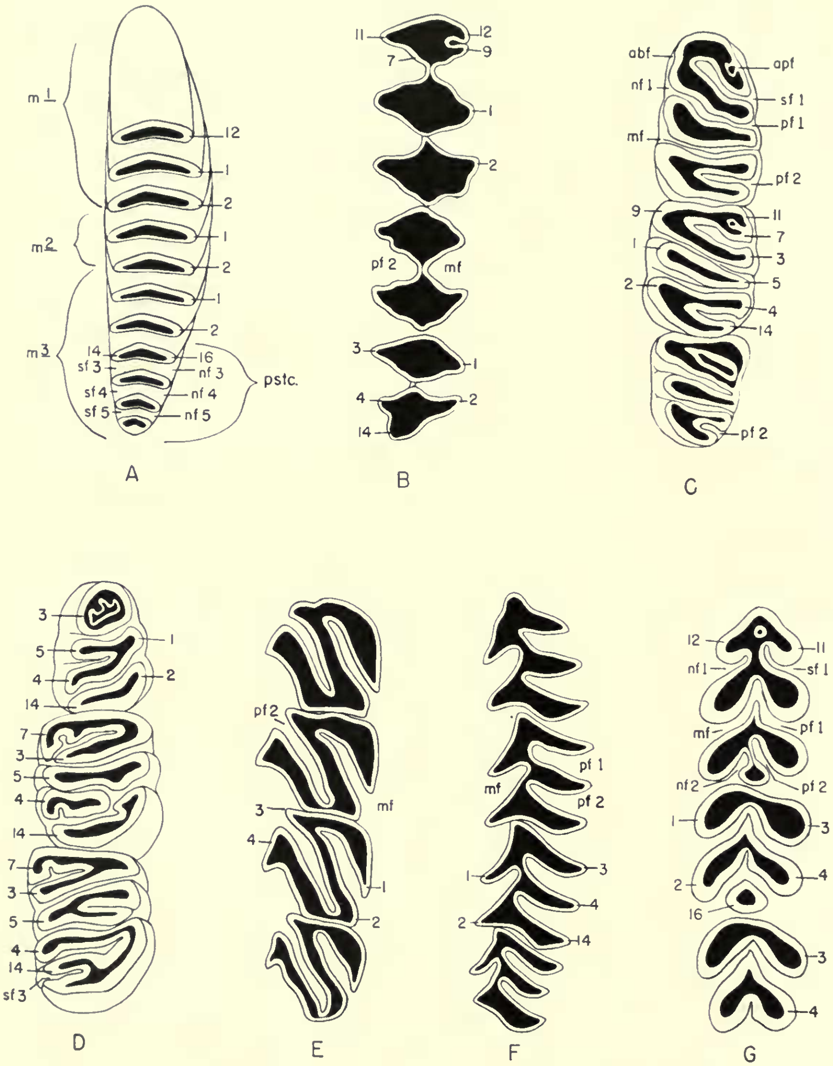
Involution

Figures 16, 17

The whole or part of a planed molar crown may be modified into a *C*-, or *E*-, or *S*-shaped pattern by varying degrees of penetration of each of the enamel folds. For this modeling process, the embryological term *involution* is used. Thus, involution, like lamination, is one of the manifestations of plication in the specialized molar.

The *C* (or $<$) pattern is derived from involution of a single lamina (partial or complete; see *Lamination* above). A double *C* (or $\overset{<}{<}$) pattern can be derived from a bi- or trilaminate molar. A *C*-shaped pattern may form, also, in third molars in which all folds except either the major or the second primary fold are obsolete or absent as a result of simplification or excessive wear. This *C*-shaped pattern of involution is not to be confused with a similar pattern formed by secondary *fusion* (see below) of two lamina on only one side of the tooth. The *C*-shaped pattern is not present in phyllotines, except sometimes secondarily in the third molar, as a result of excessive wear, rather than involution (cf. fig. 67, *g* [$m^{\underline{3}}$]).

The *sigmoid* or *S*-shaped pattern is derived from involution of a simplified molar with the procingulum and postcingulum greatly reduced or absent (fig. 69, *e*, fig. 67, *b–g* [$m_{\overline{3}}$]). A *modified sigmoid* pattern in upper molars retains indications of the first primary and, sometimes, of the second secondary folds. In the simple sigmoid pattern, first primary and second secondary folds are suppressed.


m1
m2
m3
12
1
2
1
2
1
2
14
16
sf 3
nf 3
sf 4
nf 4
sf 5
nf 5
pstc.
A
11
12
9
7
1
2
pf 2
mf
3
1
4
2
14
B
abf
apf
nf 1
sf 1
pf 1
mf
pf 2
9
11
7
1
3
5
2
4
14
pf 2
C
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1
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16
3
4
G

FIG. 16.—Lamination and involution (for names of all cusps, lophs and folds see fig. 9). See opposite page for explanation.

The sigmoid pattern in lower molars is an inverted mirror image of that of the corresponding upper molars of the same side. Sigmodont rodents are so called because of the *S*-shaped pattern of their third lower molars. In *Euneomys*, the sigmoid pattern characterizes all molars. Both sigmoid and modified sigmoid patterns occur among phyllotines.

The *E*, or *epsilon*, pattern is the sigmoid pattern with a well-developed procingulum in the upper molars and a well-developed postcingulum in the lower molars (fig. 67, *d–f* [m_2]).

Involution appears most commonly in cheek teeth in the planed, hypsodont stage of phylogeny. The process may operate before, after, or simultaneously with, the processes of lamination and triangulation.

Triangulation

Figures 16, F, 69, *c*, 115, 116

The process of *triangulation* is the modeling of circular or ovate cusps, cingula, and lophs of a planed hypsodont molar into more or less triangular-shaped elements with apices at crown borders. Tri-

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EXPLANATION OF FIGURE 16

A. Transverse lamina in the African murid (Otomyinae) *Otomys orestes* Thomas (upper right molar row). Note the supernumerary laminules and folds of the postcingulum (*pstc.*) of m^3.

B. Partial transverse lamination in the South American murid (Cricetinae) *Irenomys longicaudatus* Philippi (upper right molars). Note the 8-shaped pattern of m^2.

C. Transverse, oblique and involuted lamina in the European Miocene murid (Cricetinae?) *Neocometes brunonis* Schaub and Zapfe (lower left molars, after Schaub and Zapfe, 1953, pl. 1, fig. 13).

D. Transverse, oblique and involuted lamina in the Malagasy murid (Nesomyinae) *Gymnuromys roberti* Forsyth Major (lower right molars, after Stehlin and Schaub, 1951, fig. 577, reversed). The resemblance in enamel pattern between *Gymnuromys* and *Neocometes* is striking. However, the order of size of the molars in the former is the reverse of that in the latter and indicates that each genus may belong to a different phyletic line within the Muridae.

E. Oblique partial lamination in the West Indian caviomorph (Capromyidae) *Plagiodontia hylaeum* Miller [?=*P. aedium* F. Cuvier] (upper right premolar and molars).

F. Chevron-shaped partial lamination in the South American caviomorph (Abrocomidae) *Abrocoma bennetti* Waterhouse (lower left premolar and molars); the general pattern of the upper cheek teeth is as in B, an unusual combination.

G. Chevron-shaped lamina in the Philippine murid (Murinae) (*Crateromys schadenbergi* Meyer (lower left molars).

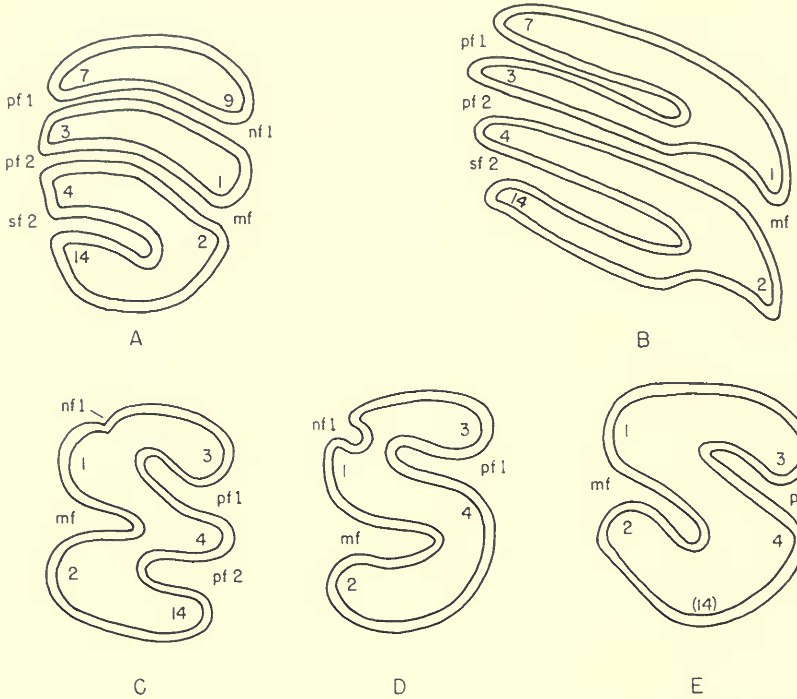

FIG. 17.—Lamination and involution (for names of all cusps, lophs and folds, see fig. 9).

A. Lamination and involution in second right upper molar of the South American caviomorph *Dinomys brannicki* Peters.

B. Lamination and involution in second right upper molar of the South American caviomorph *Dactylomys dactylinus* Desmarest.

C. Involution in second left lower molar of the South American cricetine *Phyllotis micropus*, with resultant **E**=, or epsilon pattern.

D. Involution in third left lower molar of *Phyllotis micropus*, with resultant modified **S**=pattern.

E. Involution in second left upper molar of the South American cricetine *Euneomys chinchilloides*, with resultant **S**=, or sigmoid pattern.

angulation may precede, follow, or operate simultaneously with, lamination or involution, or both, in the same tooth row. The process of triangulation has reached its highest degree of development in microtines. Good examples of triangulation also occur in the grass- and scrubland species of *Neotoma*. There are some instances of triangulation among phyllotine rodents, but *Andinomys* is the only notable example.

Fusion

Figures 10, 18

Reduction or elimination of a fold between two dental elements leads to the partial or complete *fusion* of these elements. Reduction or elimination of the elements themselves is not fusion. Individual folds are reduced by *compression* and eliminated by *isolation* and/or *coalescence*.

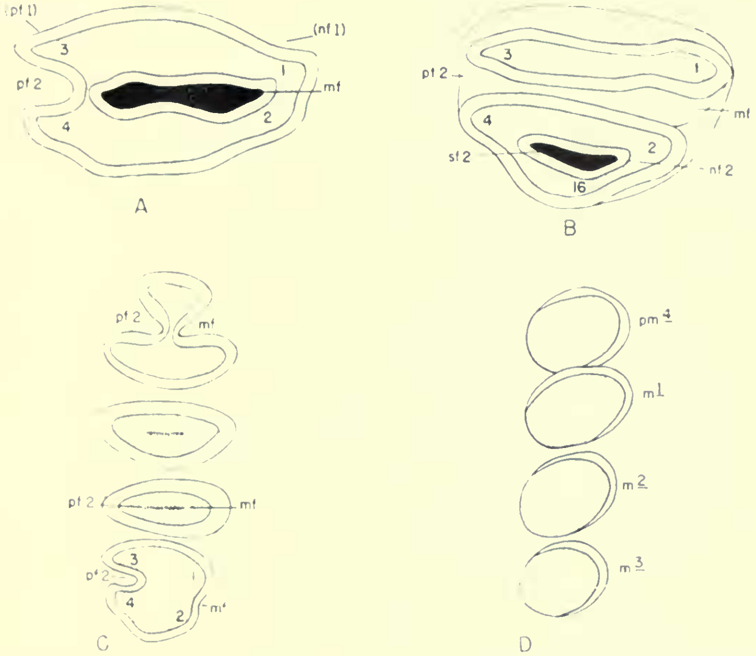

FIG. 18.—Fusion and cylindrification (for names of all cusps, lophs and folds, see fig. 9 and also compare with fig. 10).

A. Isolation of the major fold (*mf*) in the second right upper molar of the heteromyid *Dipodomys merriami* Mearns, with resultant fusion of protocone (*1*) and hypocone (*2*).

B. Lamination and fusion in second right upper molar of *Heteromys gaumeri* J. A. Allen and Chapman. Fusion of hypocone (*2*) and posteroconule (*16*) is the result of isolation of second minor fold (*nf 2*) and its coalescence with second secondary fold (*sf 2*).

C. Fusion of all cusps in first and second right upper molars of the geomyid *Orthogeomys cuniculus* Elliot as a result of isolation, compression and elimination of coalesced major fold (*mf*) and second primary fold (*pf 2*). The two molars have become cylindriform.

D. Fusion of all topographical elements in each of the upper right cheek teeth of the late Oligocene cylindrodont *Tsaganomys altaicus* Matthew and Granger, as a result of the elimination of all folds. All cheek teeth have become cylindriform.

Compression.—With advancing hypsodonty and lamination (including involution and sigmation) enamel folds tend to become narrower antero-posteriorly (cf. *Euneomys*, fig. 69, *e*). In the Lagomorpha the folds are compressed to transverse serrated lines.

Isolation.—True internal folds (fig. 9, IF) are isolated remnants of larger folds that opened on the margin of the tooth. They are present in the molars of New World pentalophodont cricetines but, with a few exceptions, have disappeared from the molars of New World tetralophodont cricetines. In pentalophodont cricetines, the first secondary fold, between paracone and mesoloph, is commonly isolated but the dental elements themselves are normally discrete, except in an extremely worn tooth. In some pentalophodont and many tetralophodont cricetines, the second secondary fold of the upper and the second primary fold of the lower molars, most frequently the third, may be mere enamel islands before they are effaced by slight attrition. Complete isolation, or loss, of the second secondary fold in tetralophodont cricetines and other rodents, results in a trilophodont molar pattern. Elimination of the second secondary and first primary of the upper molars produces the bilophodont or 8-shaped pattern. Isolation of the major and second primary folds that define the figure 8 leads to complete fusion (not loss) of all components of the primitive tri- or quadritubercular molar.

Coalescence.—Two or more folds of the *same* side of the molar may *coalesce* as a consequence of compression, isolation, or obsolescence, of a cuspule or loph. The result is the ultimate loss of the identity of one of the folds. The internal folds of pentalophodont cricetines are often coalesced with either a primary or a secondary fold. In tetralophodont cricetines, where the mesoloph is absent or obsolete, the first secondary fold is coalesced with the second primary fold and has no separate identity.

Confluence of a fold of one side of the molar with another of the opposite side, such as the union of major and primary folds in some species, results in lamination and is not coalescence. However, such confluent folds are also subject to the process of fusion. They may become compressed, isolated, and eventually eliminated.

Cylindrification

Figures 10, 18

The end product of molar evolution in most pastoral rodents and many other mammals is the cylindriform molar. This is a completely fused molar. The process of cylindrification is, therefore, an extension of *fusion.* However, the structural and time gaps between *fusion* of a secondary fold in the primitive pentalophodont molar and elimination of the major fold in a simplified prismatic molar are so great that cylindrification must be recognized as a distinct stage, the last stage, in a line of molar evolution.

Fusion and *cylindrification* are retrogressive processes as they apply to the enamel pattern of the molars. Evolution of the organism itself, however, may be progressive *pari passu* with retrogression and loss of some or all of its dentition.

Cylindrification is most common among the Edentata. The cylindrical cheek teeth of the Oligocene cylindrodontid rodent *Tsaganomys* Matthew and Granger are representative. The processes of fusion and cylindrification are well exemplified in modern forms of Heteromyidae and Geomyidae.

Differential Evolutionary Rates in Upper and Lower Molars of New World Cricetines

Evolution of each upper molar in cricetines proceeds at a different rate and does not always involve the same stages of evolution as its equivalent in the lower jaw. Evolution of the last molar, upper or lower, is more advanced than in the tooth before it. Differential rates of evolution between molars individually and between those of the upper and lower jaws collectively, result from the position of the teeth in their mortar-pestle relationship. Structural changes in the upper molars, the passive mortar, reflect the shifting movements and changing shape of the pounding, pulverizing lower molars, the pestle. Because of its terminal position, the first molar has the most varied functions, hence the most complex design. The second molar, situated at the center of the masticatory surface, has the simplest functions and is the most uniform in structure. The third molar, crowded toward the fulcrum, has a minimum use and tends to disappear altogether. This is true of cricetines but not of rodents in general (cf. fig. 16, A, D, where the third molar has evolved into the dominant tooth).

The process of planation, which normally proceeds apace with the compensatory process of hypsodonty, is usually more advanced in the upper molars. Among phyllotines, especially in *Phyllotis,* slightly terraced lower molars are commonly associated with plane upper molars. In any case, the third molar, upper or lower, is more planed than the second and the second is more planed than the first. At the same time, the upper molars may be laminating while the lower molars are undergoing triangulation or involution.

The order in which each molar element degenerates and disappears is generally the reverse of the order in which it first appeared. The older the element in phylogeny the longer it persists in the individual and in the species. The last important structural complex to formulate the cricetine pentalophodont molar, namely the fused mesoloph–mesostyle(-id) is the first to disintegrate into its components and disappear altogether. As a rule, the mesolophid disappears first, then the mesoloph. Procingulum and postcingulum break down next. However, the evolutionary relationship between these complexes in upper and lower molars is not on the same order as that existing between mesolophostyle and mesolophostylid. Although the upper procingulum is less specialized than the lower, it usually becomes obsolete first.

The original crests of the quadritubercular rodent molar are the last to be affected. The hypocone(-id) may be lost entirely but the protocone(-id), paracone, metacone(-id) and entoconid degenerate by fusion (cf. p. 99) into the cylindriform molar. The first cylindriform cricetine molar is $m_{\overline{3}}$. This tooth is also the first to disappear in more advanced murids (cf. *Desmodilliscus*, *Rhynchomys*, etc.).

The order of disappearance of enamel folds corresponds to that of the elements they define. Thus, in the upper molar, the first secondary fold is lost first, the second primary fold last.

Degeneration of molars through wear, i.e., ontogeny, follows essentially the same sequence as degeneration through phylogeny.

Third Molar

The cricetine third molar is the last to appear in ontogeny and the first to disappear in phylogeny. All evolutionary stages of simplification from pentalophodont to cylindriform molar are displayed first in the third molar. This tooth is usually terraced and frequently plane, while first and second molars are still crested. The specialized character of lamination is most frequently established first in the third upper molar. This is balanced by the appearance of sigmation in the third lower molar. The second minor fold, a novelty of the tetralophodont molar, first appears in the third molar, usually the upper. Fusion and loss of cingula and hypocone occur in the third molar, usually first in the upper, well in advance of first signs of the same degeneration in other molars.

Phylogenetically significant dental characters in the process of disappearance become progressively less evident on the crown surface of unworn teeth. Conversely, new characters in the process of establishment become progressively more evident and persist longer through wear. A mesoloph in the process of disappearance (palingenesis) and a second minor fold in the process of establishment (caenogenesis) may occur simultaneously in the unerupted or unworn third upper molar.

The third molar of most pentalophodont, or sylvan, cricetines is not functional before the animal is subadult and sexually mature. In tetralophodont, or pastoral, cricetines, including phyllotines, the third molar erupts before or shortly after birth and is functional in the juvenal mouse. Time of eruption of the third molar advances with increasing complexity of the high-crowned molar. Conversely, eruption is retarded with degeneration of the low-crowned molar.

Molar Roots

The primitive number of roots of the cricetine first molar may have been four. The roots become fewer as the tooth becomes more specialized, and the reduction in number is greater in the lower than in the upper first molar. In the following list the number of upper and lower roots of the first molar of each phyllotine species is shown:

$\frac{4}{4}$ = *Phyllotis darwini; P. griseoflavus; P. gerbillus; P. pictus; Pseudoryzomys wavrini;*
Galenomys garleppi; Eligmodontia typus; Calomys spp.

$\frac{4}{3-4}$ = *Phyllotis amicus.*

$\frac{4}{3}$ = *Phyllotis sublimis; P. micropus; Calomys* spp.

$\frac{3-4}{3}$ = *Phyllotis boliviensis.*

$\frac{3-4}{2-3}$ = *Zygodontomys* spp.

$\frac{2}{2}$ = *Andinomys edax; Chinchillula sahamae.*

Upper Incisor

Figures 19, 20

The generalized upper incisor of rodents is slender or moderately thickened, with the terminal half slightly recurved and the cutting edge lying on a horizontal plane or at a slight angle. The anterior face is smooth and normally pigmented yellow, orange or reddish. As a rule, the vertical length, measured in front, is about one-half the length of the diastema. The generalized upper incisor, common to most rodents, has been drastically modified in many species.

The specialized upper incisor may be markedly thick or slender, extremely recurved (opisthodont), straightened (orthodont), thrust forward (proodont), or flexed inwardly. The anterior face may be unpigmented, grooved, or striated. The cutting edge may be acutely angular, and the whole tooth may be disproportionately lengthened or shortened. All modifications of the upper incisor are related to molar specialization. In many cases, a correlation with modifications of the palate is obvious. A few of the more striking divergents from the generalized form of the upper incisor are described in the following.

Degenerative.—The upper incisor may degenerate progressively with deterioration of the cheek teeth. This process is generally associated with a compensatory elongation and attenuation of the muzzle, especially notable in the diastemal portion of the palate. Incisor degeneration has not occurred among phyllotines. Other murids, however, afford examples. The upper incisor of the Celebesian *Echiothrix leucura* Gray is short, weak, faintly grooved and orthodont. The diastemal portion of the palate in this species is elongate. The diastema of the lower jaw, however, is not proportionately produced but the very long slender lower incisor bridges the gap to make occlusion. The inner row of cuspules of the upper molars are reduced and the corresponding ones of the outer side of the lower molars are obsolete or fused.[1] The process of incisor degeneration associated with loss of pigmentation, diastemal elongation, and molar degeneration is extreme in the Philippine shrew rat *Rhynchomys soricoides* Thomas (fig. 20, A–C). Here, the first and second molars of upper and lower jaws are practically functionless, the third molars have disappeared and the lower incisors are short and extremely fine. In all, the maxillo-mandibular region approaches the condition existing in the xenarthrous and monotreme anteaters. Rodents of the type described are small-eyed burrowers. They probably feed mainly on earthworms and grubs in addition to soft, ripe fruit.

Seizer-digger.—The upper incisor may increase its utility while the cheek teeth become simplified in form, specialized in function, and reduced in number. The highly specialized seizer-digger incisor

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[1] This condition simulates a reversal from the typical triserial cuspidate pattern of murines to the biserial arrangement characteristic of cricetines.

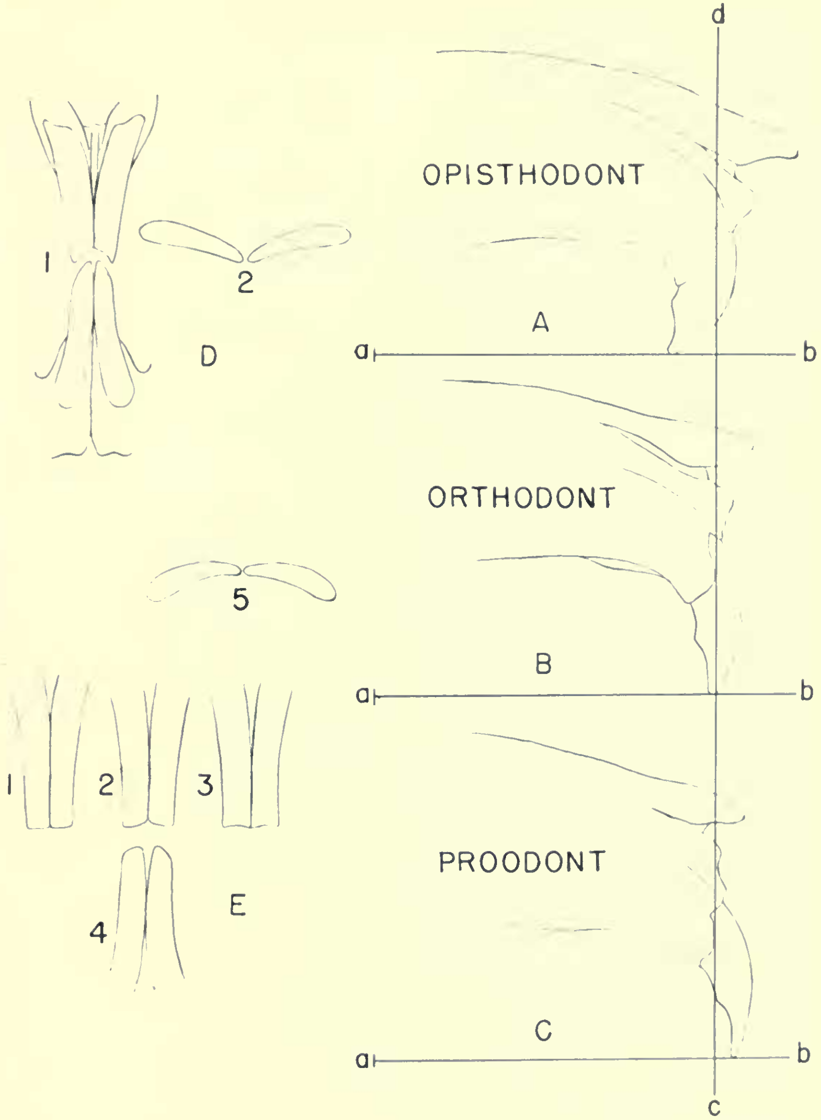
d
OPISTHODONT
A
a
b
ORTHODONT
B
a
b
PROODONT
C
a
b
c
1
2
D
5
1
2
3
4
E

FIG. 19.—Forms of incisors in phyllotines: A–C, curvatures with reference to the basal-incisive plane (*a*–*b*) and vertical-incisive plane (*c*–*d*). D, incisors of *Andinomys edax:* 1, front view of upper and lower incisors; 2, cross section of upper incisors above cutting edge. E, incisors of *Phyllotis darwini:* 1–3, variation in outline of cutting edge of upper incisors; 4, lower incisor; 5, cross section of upper incisor above cutting edge.

is, as a rule, slender, markedly elongate, proodont, slightly or not at all scored longitudinally on its anterior face, and lightly or not at all pigmented (fig. 20, D). It is adapted for use as a pick in digging and for cropping short shoots or seizing small insects, larvae, and earthworms in tunnels or in rocky or cavernous situations where the hands are of little or no assistance. The gnawing power of the seizer-digger is probably reduced. The diastemal portion of the palate in rodents with this type may be long or short but is always attenuate.

Phyllotines with specialized seizer-digger upper incisors are *Galenomys*, *Phyllotis boliviensis* and individuals of *P. sublimis* (figs. 59, 62). Some species of murines combine moderately elongated proodont upper incisors of the seizer-digger type with an elongation of the diastemal portion of the palate. In these, the mandibular diastema remains short while the lower incisor lengthens extraordinarily to make occlusion with the upper. The Burmese and Assamese *Rattus manipulus* Thomas is a moderately specialized example of this type with molar degeneration incipient. According to Roonwal (1949, p. 100) this is a burrowing rat that feeds largely on insects and earthworms. The seizer-digger characters are more advanced in the incisor of the Philippine striped rat, *Chrotomys whiteheadi* Thomas. Its molars are more simple, with the third nearly vestigial. This animal is also an earthworm eater (Rabor, 1955, p. 207). The closely related Philippine rat, *Celaenomys silaceus* Thomas, is even more specialized in the same direction. Both *Chrotomys* and *Celaenomys* are divergents from the same murine stock that gave rise to *Rhynchomys*. They are much less nearly related to *Hydromys* with which they are currently associated in the superfluous subfamily Hydromyinae. Extreme examples of the seizer-digger incisor occur in such unrelated rodents as the Andean cavy (*Monticavia*), the Chilean coruro (*Spalacopus*), the viscachas (*Lagostomus*), the African mole rat (*Cryptomys*), the Asiatic burrowing vole (*Ellobius*) (fig. 20, D), and the Oregon gopher, *Thomomys bulbivorus*. In all, the incisors are wholly or partially unpigmented.

Triturator.—The specialized triturator incisor is short or long, orthodont or opisthodont, thick, often deeply grooved longitudinally and usually well pigmented (fig. 20, E). Triturators are efficient gnawers, choppers, and whittlers, and they function as hoes if used in digging. Triturators supplement, and may tend to usurp, the grinding function of cheek teeth. The diastemal portion of the palate of rodents with the triturator type of incisor tends to become thick and shorter relative to the basicranial length. The upper in-

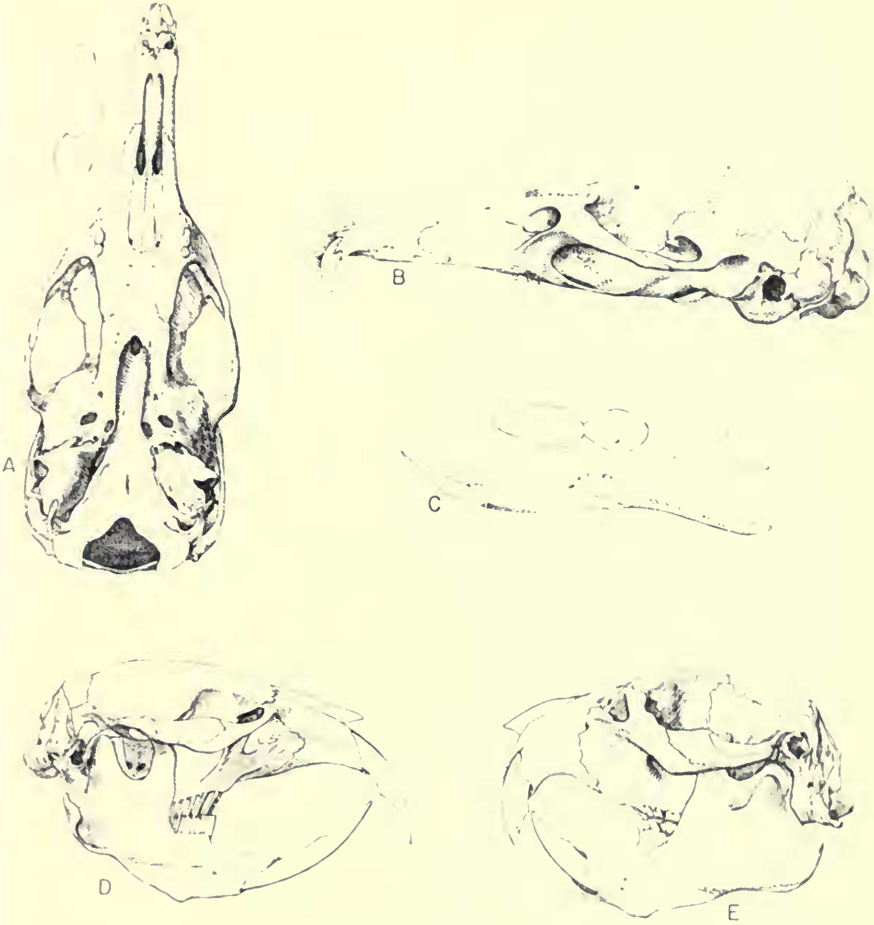

Fig. 20.—Rodent incisors: A, *degenerative* type in the murid (Rhynchomyinae) *Rhynchomys soricoides* Thomas, palatal aspect showing long palate and right upper molars; B, side view of same skull; C, mandible and left lower molars of same; D, *seizer-digger* type in the murid (Microtinae) *Ellobius talpinus* Pallas; E, *triturator* type in the muroid (Rhyzomyidae) *Rhizomys pruinosus* Blyth.

cisor of some fossorial forms such as the African *Tachyoryctes* and the Indo-Chinese *Nyctoleptes*, combine the special digging qualities of both triturator and seizer-digger types. Their incisors are elongate, forward-projecting, thick and heavily pigmented.

The triturating type of upper incisor is not highly developed in phyllotines. The orthodont upper incisor of *Chinchillula sahamae* is comparatively heavy but not definitely classifiable as a specialized triturator. The upper incisor of *Phyllotis micropus* is the heaviest in the genus but is still very near the generalized type. Incisors of *Calomys, Eligmodontia, Zygodontomys* and the species of *Phyllotis,* other than the one mentioned above, are generalized. Many examples of highly specialized triturators occur in geomyids, bathyergids, caviomorphs and castorids. The example figured (fig. 20, E) is of the Asiatic bamboo rat, *Rhizomys pruinosus.*

Flexed.—The upper incisor of *Andinomys* (fig. 19, D) is inwardly flexed, its cutting edge oblique with the sharp point on the outer side. The paired incisors form a two-pronged instrument. The tips of the lower incisors taper to a point that fits the angle between the upper incisors. Incisors of certain fish-eaters (*Ichthyomys, Anotomys*), the African dormouse (*Claviglis*), and the tortoise-headed rat (*Lophiomys*) are of the same type. In *Rhagomys* and the wood rat (*Neotoma*), the cutting edge of the upper incisors also forms prongs but the teeth are not flexed inwardly. Even more remarkable than the shape of the incisors is the great diversity in the form and feeding habits of the many species of rodents to which they are common.

Grooved.—Grooves or striations on the anterior face of the upper incisors occur sporadically throughout the Rodentia. Their function or structural significance is unknown. With the exception of *Aporodon,* grooves or striations are normally found only among tetralophodont rodents. They are often present and usually well defined in the specialized triturating type of incisor but are absent or poorly defined in the seizer-digger type.

The systematic significance of grooved incisors in murids is slight or nil. Nevertheless, their appeal as obvious "key characters" is great. At one time or another the name *Reithrodon,* used for a monotypic genus of groove-incisored cricetines, was applied to such diverse, groove-incisored forms as *Phyllotis pictus, Sigmodon alstoni, Irenomys longicaudatus, Euneomys chinchilloides, Chelemyscus fossor,* and some species of *Reithrodontomys.*

Among phyllotines, incisors of some individuals of *Phyllotis boliviensis* are scored by longitudinal striae hardly or not at all visible to the naked eye. In *P. sublimis* distinct striae are usually present and in *P. pictus* striae are constantly present and usually well defined. Striae are sometimes found in the upper incisors of *Chinchillula sahamae.* In *Euneomys,* a genus nearly related to phyllotines, the incisor is deeply grooved and of the triturator type.

Lower Incisor

Variation in length, shape, form of cutting edge, and angle of projection of the lower incisor is correlated with mandibular mobility, the size and shape of the mandibular processes, and the structure of the muzzle as a whole. Upper and lower incisors, therefore, do not show as close a morphological correspondence as exists between upper and lower molars.[1] Analysis of variation in the cricetine lower incisor and the interpretation of its significance are subjects that have not been studied. However, the description of the mandible of each species in the following pages includes a reference to the degree of projection of the lower incisor root. Also, the length and angle of the exposed anterior portion of the lower incisor are noted in the description of *Galenomys* (p. 464, fig. 63), in comparisons between *Phyllotis* and the African *Mystromys* (p. 221, fig. 60), and in the general discussion of the upper incisor in the preceding section.

Grooving of the lower incisors is rare in murids, absent in cricetines. Where it does occur, as in the African *Otomys*, it is a variable character and is normally associated with the grooved triturator type of upper incisors.

Incisor Indices

Relationship of the incisors, upper or lower, to the molar plane and to the basal-incisive plane (see definitions below) varies from species to species. Characters revealed by measurements of these planes are not described in the text (see figs. 59, 60, 62, 63).

Planes of reference used in the illustrations are defined as follows (figs. 19, 21):

Basal-incisive plane.—Defined by a line from the tips of the upper incisors to the most inferior point of the basicranium (basioccipital, tympanic bulla, paroccipital process, or pterygoid, as the case may be).

Vertical-incisive plane.—Defined by a line projected through, or tangential to, the upper or lower incisor and vertical to the basal-incisive or -mandibular plane.

Basal-mandibular plane.—Defined as the line projected by those parts of the inferior border of the mandible that are in contact with a plane surface.

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[1] There is no foundation for surmising, as does Landry (1957, p. 223), that rodents seem to have "evolved a stable lower incisor form and variously adapted the upper incisor and rostrum to fit it."

Molar plane.—Defined by a line connecting the peak of the first cheek tooth with the peak of the last cheek tooth of either upper or lower jaw.

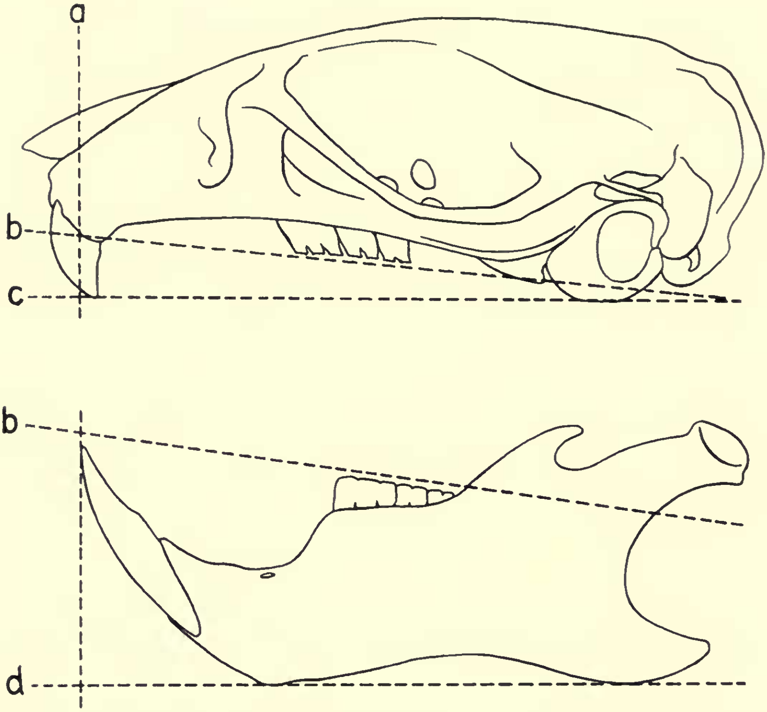

FIG. 21.—Side view of skull, showing incisive and molar planes: *a*, vertical-incisive plane; *b*, molar plane; *c*, basal-incisive plane; *d*, mandibular plane.

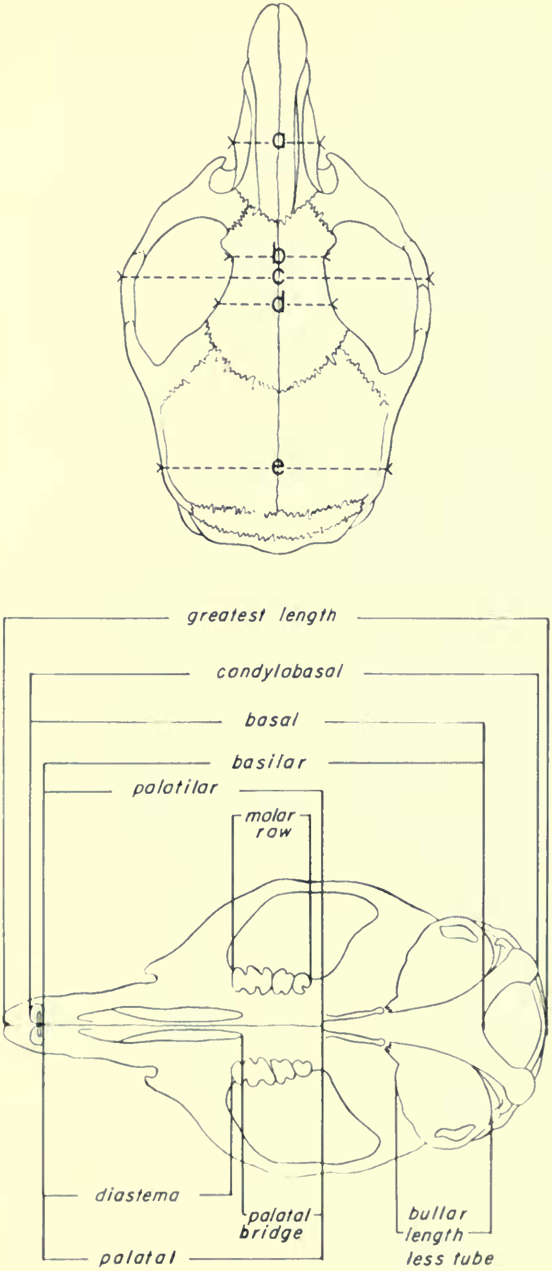
a
b
c
d
e
greatest length
condylobasal
basal
basilar
palatilar
molar row
diastema
palatal bridge
palatal
bullar length less tube

FIG. 22.—Dorsal and palatal aspects of skull, showing cranial measurements used in text. *a*, width of rostrum; *b*, least interorbital breadth; *c*, zygomatic breadth; *d*, mid-frontal width; *e*, width of braincase.

EXPLANATION OF FIGURES 23–25

1. Nasal
2. Frontal
3. Parietal
4. Interparietal
5. Occipital
6. Premaxillary
7. Maxillary
8. Jugal
9. Squamosal or temporal
10. Palatine
11. Presphenoid
12. Basisphenoid
13. Parapterygoid plate (often fused to basisphenoid)
14. Pterygoid process (often fused to basisphenoid)
15. Alisphenoid (more or less fenestrated)
16. Auditory, or tympanic, bulla
17. Mastoidal, or periotic, capsule, or petrosal
18. Orbitosphenoid
19. Lachrymal

a. Capsular projection for upper incisor
b. Preorbital foramen
c. Antorbital, or infraorbital, foramen
d. Antorbital bridge (of maxillary)
e. Incisive, or anterior palatal, foramen
f. Palatal process of premaxillary
g. Palatal process of maxillary
h. Anterior palatal pit (and foramen)
i. Posterolateral palatal pit (and foramen)
j. Parapterygoid fossa
k. Sphenopalatine vacuity
l. Mesopterygoid fossa (between pterygoid processes)
m. Hamular process of pterygoid
o. Petrotympanic fissure
p. Foramen ovale
q. Auditory bullar tube (eustachian canal)
r. Auditory meatus
s. Occipital condyle
t. Foramen magnum
u. Paroccipital process
v. Glenoid fossa
w. Carotid canal and fissures
x. Mastoidal process
y. Lambdoidal crest
z. Temporal ridge

aa. Optic foramen
bb. Sphenopalatine foramen
cc. Anterior lacerated foramen
dd. Zygomatic plate (of maxillary)
ee. Hamular process of squamosal
ff. Temporal vacuity (dorsal and ventral)

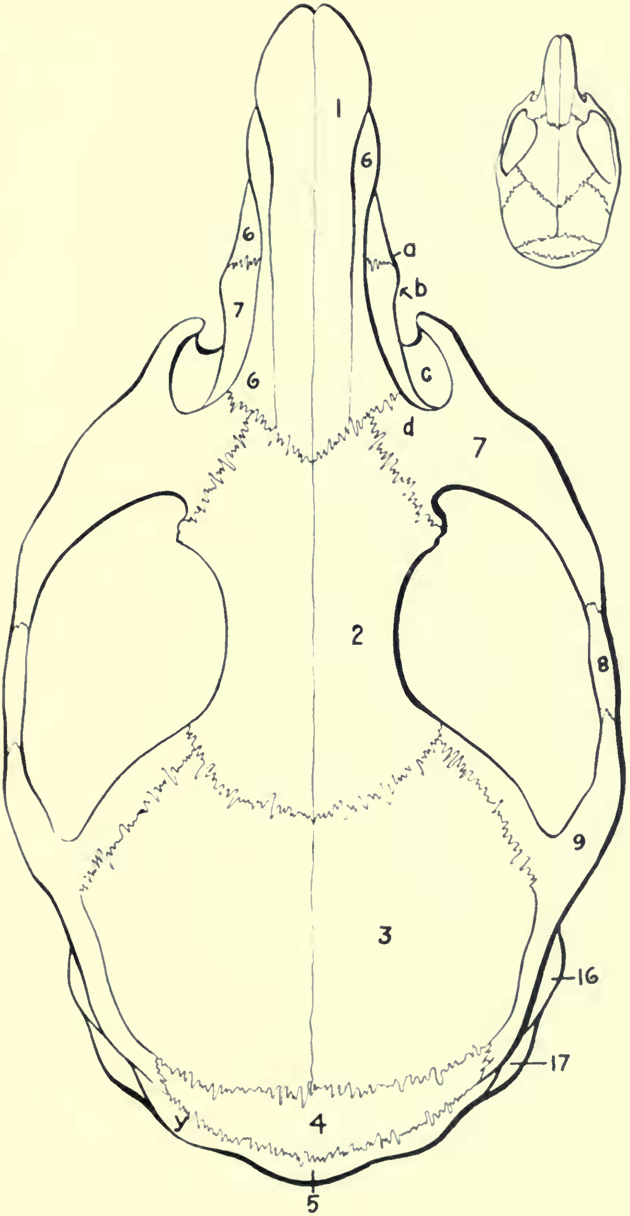
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FIG. 23.—Parts of the dorsal aspect of a murid skull. Small figure shows divergent-sided frontals and angular fronto-parietal sutures. See p. 110 for key to numbers and letters.

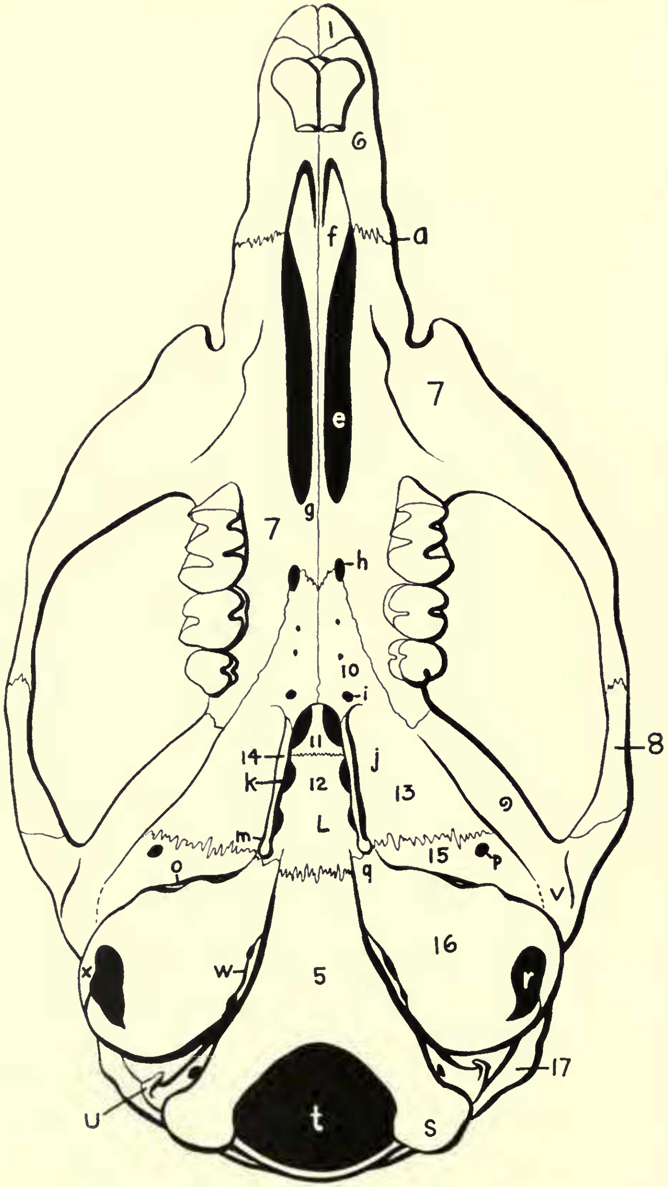
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FIG. 24.—Parts of the ventral aspect of a murid skull. See p. 110 for key to numbers and letters.

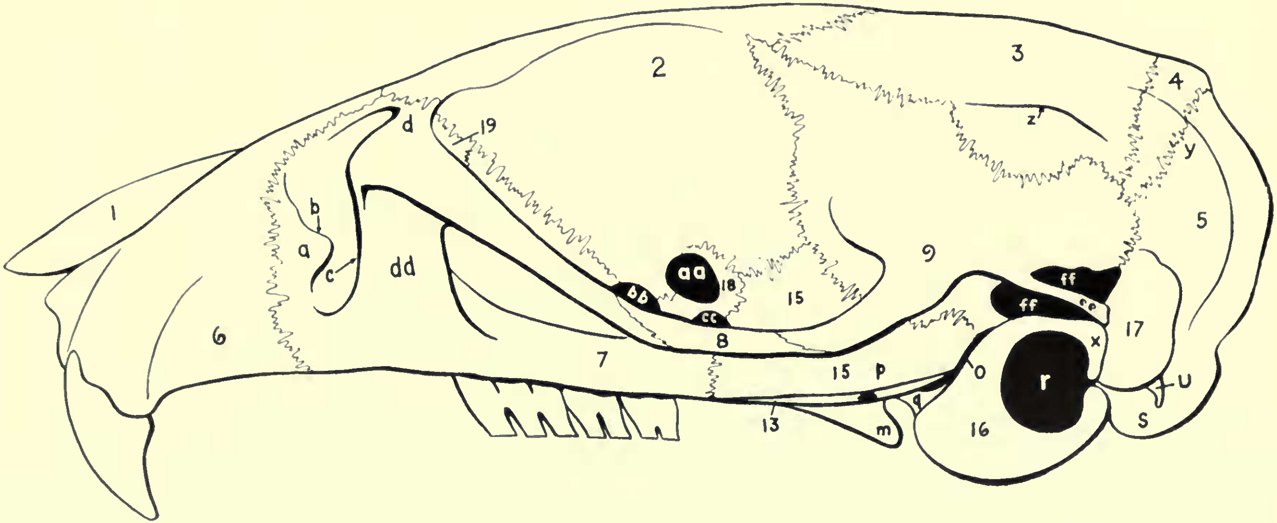
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Fig. 25.—Parts of the lateral aspect of a murid skull. See p. 110 for key to numbers and letters.

EXPLANATION OF FIGURE 26

a. Ramus
b. Angular process
c. Condyloid process
d. Coronoid process
e. Capsular projection
f. Sigmoid notch
g. Mental foramen
h. Inferior masseteric ridge
i. Superior masseteric ridge
j. Mandibular foramen
k. Symphysis

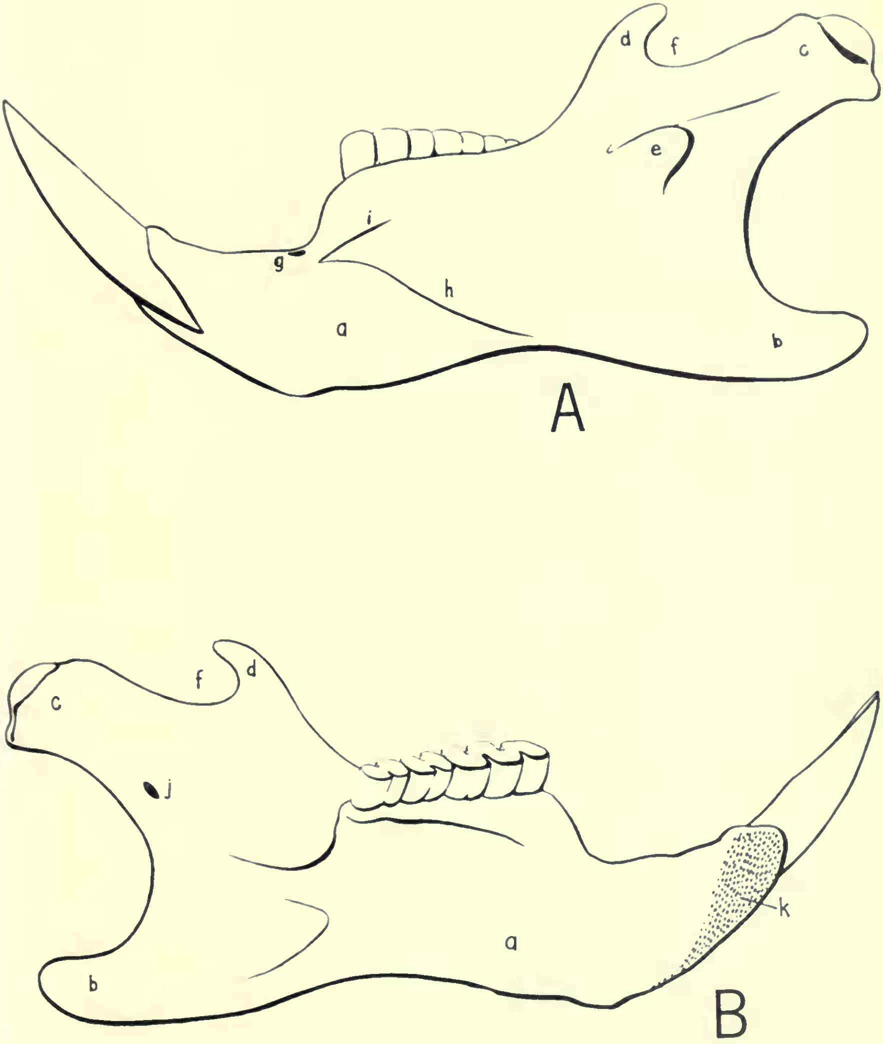
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FIG. 26.—Parts of the mandible of a murid. A, lateral aspect; B, medial aspect. See p. 114 for key to letters.

SYSTEMATIC REVISION OF PHYLLOTINES

Characters of the Phyllotine Group of Cricetine Rodents

External characters.—Body and limbs adapted for terrestrial life with normal ambulatory, slightly saltatorial, scansorial or natatorial movements; notable specializations for burrowing, jumping, climbing or swimming absent; body size varying from extremely small to moderately large for cricetines; pelage normally thick, the individual hairs long, fine and soft to moderately coarse, never hispid or spiny; juvenal pelage usually similar in color and texture to adult pelage; color of nose, ears and rump not reddish or in marked contrast with remainder of upper parts; tail from less than one-half of combined head and body length to one and one-half times longer, moderately to well haired, often pencilled and faintly or sharply bicolor for at least two-thirds of its length; eyes normal; ears moderate to large in size, always more than one-half of length of hind foot; hind foot (fig. 3) not markedly enlarged, well haired above, heel beneath hairy, plantar surface bare or hairy; pollex with nail; claws of fore and hind feet not specially modified, the middle claw, measured on ventral surface, one-half or less of length of corresponding digit.

Cranial characters (figs. 22–26).—Palatal bridge produced posteriorly to or behind posterior plane of last molars, posterior border rounded or square, with or without a short median spine; posterolateral portion of each palatine bone often excavated or depressed and always marked by a distinct perforation or by a reticulation of perforations or pits; mesopterygoid fossa more or less ∩-shaped or M-shaped, the pterygoid processes parallel-sided or slightly divergent posteriorly, but never defining a sharp Λ-shaped fossa along their entire length; parapterygoid fossa, seen from ventral surface, usually shallow and subtriangular or ovate in outline, lateral wall not parallel to inner wall (hamular process) but gradually merged into dorsal surface and anterior wall; anterior wall of parapteryoid fossa usually flattened, rarely undercut to form a deep fossa; sphenopalatine vacuities usually large, the lateral wings of the basisphenoid and presphenoid thinly ossified and largely fenestrated; incisive foramina long and narrow, pointed behind and, with few individual exceptions, extending posteriorly to or behind anterior plane of first molars; rostrum not markedly tapered dorso-ventrally from base to tip; anterior process of premaxillary projected slightly or not at all beyond antero-vertical plane of incisors and never united with antero-lateral border of nasals to form a tubular projection or trumpet; portion of premaxillo-maxillary suture below antorbital foramen situated about midway between first molar and incisor and forming a 90°–135° angle to horizontal plane of palate; nasals behind roughly square, rounded or obtusely triangular, terminating from slightly in front of to slightly behind fronto-maxillary suture, never with a long pointed process extending deeply between frontals; supraorbital edges square, ridged, beaded or produced as ledges, never evenly curved; zygomatic arches complete; interparietal well developed, at least transversely, and with a distinct suture separating each of its borders from at least two-thirds of the width of parietal and occipital, respectively; opening of antorbital foramen on dorsal surface deeply excised, semicircular or ovate in outline, with more than one-half to nearly full width of zygomatic plate clearly exposed to view when seen from above; inner side of medio-lateral axis of antorbital bridge of zygoma never directed posteriorly; zygomatic plate comparatively high and broad, width more than one-half of least interorbital breadth, anterior border plane, slightly convex, concave, or, if deeply excised and provided with prominent spine on upper corner, the incisors not grooved.

Dental characters.—Molars well developed, mesoloph(id) absent or vestigial, at least in $m\frac{1}{1}-\frac{2}{3}$; mesostyle(id) when present never fused with mesoloph(id); ectoloph, enteroloph and second minor folds absent; first upper molar with three or four roots, lower with two to four roots; occlusal surface of m^2 square or broadly rectangular in outline, its width at posterior half approximately two-thirds or more of greatest length of tooth; third molar usually fully erupted and functional in active juvenals; m^3 from one-half to three-fourths of length of m^2; procingulum of m_1 not isolated from cusps by confluence of first minor and first secondary folds; major and primary folds well opened, not compressed antero-posteriorly; first primary fold of m^3 reduced or absent, its length, when present, one-half or less of combined length of second primary and internal folds (usually fused except, frequently, in *Calomys*), long axis of second primary fold inflected forward, second secondary fold reduced to a small enamel island, or absent; second primary fold of m_3 obsolete or absent; outer surface of each incisor smooth or marked by one or two weakly defined grooves.

KEY TO SECTIONS, GENERA AND SPECIES OF PHYLLOTINE RODENTS

1. Upper incisors orthodont, proodont, or opisthodont, with anterior surface smooth, grooved or striated; upper molars high or low crowned, with flat or terraced grinding surfaces, the anterior enamel walls of at least the inner upper and outer lower cusps not thrust upward and back to form rounded crests; procingulum of $m^{\underline{1}}$ simple or bilobate, its occlusal surface flat, laminate, subtriangular, or subcordate in outline; mesostyle absent or extremely rudimentary; ear, measured from notch, shorter to longer than hind foot; mammae never more than 8 (*PHYLLOTIS* section)..............................4

1. Upper incisors opisthodont, their anterior surface never marked by vertical grooves or striae; upper first and second molars low or moderately high crowned with crested surfaces, the anterior enamel wall of each of the four principal cusps and of procingulum of $m^{\underline{1}}$ thrust upward and inclined posteriorward to form well-defined rounded crests in unworn tooth; procingulum of $m^{\underline{1}}$ uniconulate or biconulate, its outline in worn tooth broadly ovate with or without an anterior notch; mesostyle present or absent, when present usually fused with paracone. Ear, measured from notch, never longer than hind foot; toes of hind foot variable in length; mammae 6 to 14 (*CALOMYS* section).............2

2. Mesopterygoid fossa as wide as or wider than parapterygoid fossa measured at same plane; sides of supraorbital region markedly divergent, the edges strongly beaded. $m^{\underline{1}}$ with or without anterior median fold, the procingulum never clearly divided into two conules in adult; mesostyle often well developed and fused with paracone; $m_{\overline{3}}$ nearly as long as to slightly longer than $m_{\overline{2}}$. Fifth hind toe short, its tip, less claw, not reaching distal end of first phalanx of fourth toe; mammae 8..........................*Zygodontomys* (p. 196)

2. Mesopterygoid fossa narrow, its width less than width of parapterygoid fossa measured at same plane; sides of supraorbital region divergent or nearly parallel-sided, the edges beaded or square. $m^{\underline{1}}$ with or without anterior fold, procingulum uniconulate or biconulate; $m_{\overline{3}}$ distinctly shorter than $m_{\overline{2}}$; mesostyle absent or extremely rudimentary. Fifth hind toe long or short; mammae 6 to 14...3

3. Sole with three middle postdigital tubercles more or less united to form a thickly haired cushion; first postdigital tubercle small, naked; fifth postdigital tubercle reduced or absent; tarsal tubercle small, naked; fifth hind toe long, its tip, less claw, reaching distal end of first phalanx of fourth toe or beyond.
Eligmodontia (p. 175)

3. Sole with six well-defined, naked plantar tubercles; fifth hind toe, less claw, barely or not extending as far as distal end of first phalanx of fourth toe.
Calomys (p. 123)

4. Sole with three middle postdigital tubercles coalesced to form a thick, well-haired pad; size small, greatest length of skull less than 28 mm.; incisors opisthodont, never grooved........................*Eligmodontia* (p. 175)

(Individuals with extremely worn molars may be confused with the *Phyllotis* section, hence *Eligmodontia* is keyed in this as well as in the *Calomys* section where it belongs.)

4. Sole with three middle postdigital tubercles discrete or partially fused at their base, the tubercles (not surrounding area) entirely naked or set with a few short inconspicuous bristles; length of skull variable; angle of incisors variable, their anterior face smooth or grooved.......................................5

5. Upper incisors opisthodont, ungrooved; zygomatic breadth not more than distance from posterior tips of nasals to anterior border of interparietal; interorbital breadth at mid-frontal plane less than greatest width of rostrum; sides of supraorbital region divergent and slightly ridged or beaded; mesopterygoid fossa at base of hamular processes at least as wide as parapterygoid fossa measured at same plane; sole, including plantar surface of heel, entirely bare; fifth hind toe, less claw, not reaching distal end of first phalanx of fourth; first hind toe, less claw, not reaching base of first phalanx of second toe; ear, measured

from notch, less than 70 per cent of hind foot length; tail sparsely haired, untufted, and not markedly elongated or shortened.
Pseudoryzomys wavrini (p. 208)

5. Upper incisors orthodont, proodont or opisthodont, grooved or smooth, zygomatic breadth more than distance from posterior tips of nasals to anterior border of interparietal; interorbital breadth at mid-frontal plane more or less than greatest width of rostrum; sides of supraorbital region variable, the edges square, beaded or ridged; width of mesopterygoid fossa variable; plantar surface of heel hirsute, remainder of sole with or without hair; fifth hind toe long, its tip, less claw, extending to distal end of first phalanx of fourth toe; first hind toe, less claw, reaching at least to base of first phalanx of second toe; ear measured from notch, more or less than 70 per cent of hind foot length; tail variable in length, more or less hirsute, with or without a terminal tuft......6

6. Supraorbital region comparatively broad, the sides diverging from slightly behind angle of fronto-maxillary suture; interorbital breadth at mid-frontal plane more than greatest width of rostrum; supraorbital edges square or beaded, with or without projecting ledges....................................7

6. Supraorbital region narrow, the sides either parallel or convergent from slightly behind angle of fronto-maxillary suture to form constriction at approximately mid-frontal plane; interorbital breadth at mid-frontal plane equal to or, usually, less than greatest width of rostrum; supraorbital edges square, pinched or, sometimes, weakly beaded or with projecting ledges.....................11

7. Size large, greatest length of skull in fully adult more than 30 mm., width of braincase more than 13 mm., alveolar length of molar row 5 mm. or more, antero-posterior length of bulla (less tube) more than 5 mm.
Phyllotis griseoflavus (p. 441)
(Also "*Graomys edithae*" Thomas, p. 461)

7. Size small, greatest length of skull less than 30 mm., width of braincase less than 13.2 mm., alveolar length of molar row less than 5 mm., antero-posterior length of bulla (less tube) 5 mm. or less..............................8

8. Bullae little inflated, their antero-posterior length (less tube) approximately equal to or less than length of molar row...................*Calomys* (p. 123)

(Individuals with extremely worn molars may be confused with species of the *Phyllotis* section, hence *Calomys* is keyed here as well as in the section with crested molars.)

8. Bullae well inflated, their antero-posterior length (less tube) always more than length of molar row..9

9. Habitat in western Peru..10

9. Habitat in northern Andes of Argentina.........*Phyllotis hypogaeus* (p. 462)
(See also "*Graomys edithae*" Thomas, p. 461)

10. Ears, from notch, more than 20 mm., hairs of under parts and thighs not wholly white...............................*Phyllotis amicus* (p. 438)

10. Ears, from notch, less than 20 mm., hairs of under parts and thighs wholly white....................................*Phyllotis gerbillus* (p. 430)

11. Anterior face of each incisor marked by one or two vertical grooves, visible to the unaided eye...12

11. Anterior face of each upper incisor not grooved though often with fine vertical striae hardly or not at all perceptible to the unaided eye...............14

12. Second upper molar with major and second primary folds extending obliquely beyond midline of tooth; procingulum reduced (obsolete or absent in worn tooth), the occlusal surface forming an S-shaped pattern; upper molar row markedly divergent posteriorly; incisors opisthodont; postero-lateral palatine excavations deep and greatly enlarged antero-posteriorly..*Euneomys* (p. 493)

12. Second upper molar with major and second primary folds not extending beyond midline of tooth; major fold in worn tooth more or less at right angles to midline; outline of occlusal surface of moderately worn tooth more or less 8-shaped, with or without a notch in upper outer corner to mark position of procingulum; upper molar row more or less parallel-sided; incisors orthodont to proodont; postero-lateral palatine excavations not markedly developed . . 13

13. Tail less than 70 mm. and less than 65 per cent of combined head and body length; hind foot (dry, with claw) less than 25 mm. . . *Phyllotis sublimis* (p. 419)

13. Tail more than 70 mm. and more than 55 per cent of combined head and body length; hind foot (dry, with claw) usually more than 25 mm. *Phyllotis pictus* (p. 404)

14. Alveolar length of molar row more than 6.6 mm. 15

14. Alveolar length of molar row less than 6.6 mm. 17

15. Incisors orthodont or slightly opisthodont; second upper molar with procingulum obsolete or absent; primary and major folds of m^2 penetrating as far as but not beyond midline of tooth; white of hips and lower sides of rump separated by black of outer sides of thighs . . . . *Chinchillula sahamae* (p. 415)

15. Incisors opisthodont; second upper molar with procingulum well developed; second primary fold of m^2 penetrating beyond midline of tooth and apex of major fold; hips, rump and outer sides of thighs more or less uniformly colored buff to brown 16

16. Medial anterior borders of upper incisors meeting to form a broadly angular trough when seen in cross section; palatine bones deeply excavated postero-laterally; cusps of first two upper molars triangular in outline and arranged in zigzag pattern. Habitat, Andes of Peru, Bolivia and northern Argentina. *Andinomys edax* (p. 472)

16. Medial borders of upper incisors meeting in midline to form a convex outline when seen in cross section; palatine bones slightly or not at all excavated postero-laterally; cusps of first two upper molars elliptical or ovate in outline with those of outer side nearly or quite opposite their analogues of inner side. Habitat, Andes of southern Chile and southern Argentina. *Phyllotis micropus* (p. 391)

17. Plantar surface of hind foot well haired; skull markedly vaulted mid-dorsally. *Galenomys* (p. 464)

17. Plantar surface of hind foot bare; dorsal contour of skull flat or slightly convex, not vaulted 18

18. Procingulum of m^2 reduced or obsolete, of m^3 obsolete or absent; incisors opisthodont, their anterior aspects smooth; greatest zygomatic breadth nearly always less than distance from tips of nasals to posterior borders of last molars; tail from about 40 per cent shorter to over 25 per cent longer than combined head and body length 19

18. Procingulum of m^2 well developed and persistent except in greatly worn tooth, of m^3 present but not always well developed; incisors proodont, orthodont or opisthodont, with or without vertical striae or weakly defined grooves on anterior aspects; greatest zygomatic breadth more or less than distance from tips of nasals to posterior border of last molars; tail always shorter than combined head and body length 20

19. Upper incisors slender, combined width of upper cutting edges less than alveolar length of m^1; molar rows parallel-sided or slightly convergent or divergent posteriorly; lower first molar 4-rooted; zygomata not greatly expanded, tending to be parallel-sided, their greatest breadth less than distance between posterior tips of nasals and anterior border of supraoccipital; tail longer or shorter than combined head and body length. *Phyllotis darwini* complex (p. 234)

19. Upper incisors thick, combined width of cutting edges equal to or more than alveolar length of m^1; molar rows usually divergent posteriorly; lower first molar 3-rooted; zygomata well expanded posteriorly, the sides usually markedly divergent antero-posteriorly, giving a triangular outline to midcranial region; greatest breadth across zygomatic arches subequal to distance between posterior tips of nasals and anterior border of supraoccipital; tail always shorter than combined head and body length. *Phyllotis micropus* (p. 391)

20. Upper incisors ungrooved, opisthodont; tail longer or shorter than combined head and body length 19

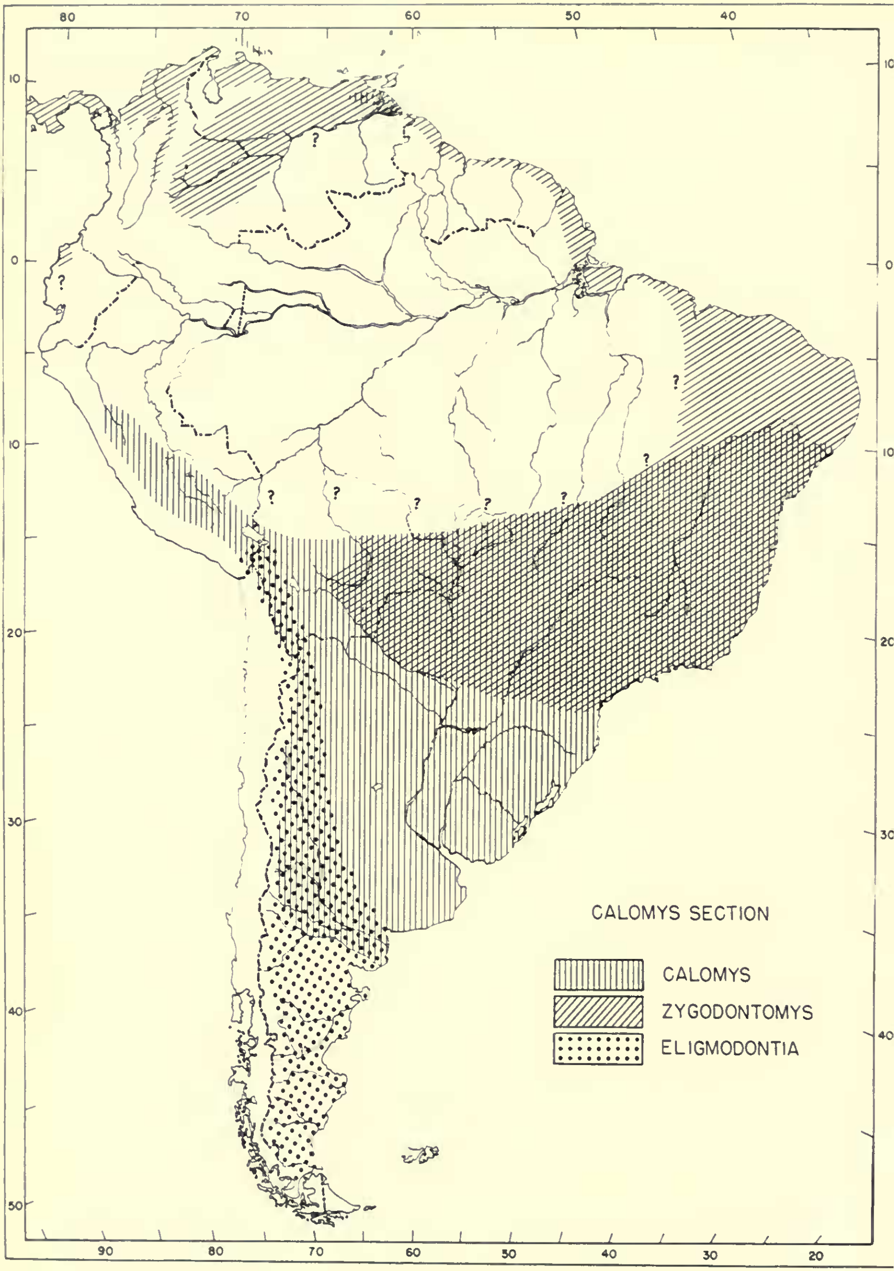
20. Upper incisors ungrooved or grooved, proodont or orthodont; tail always shorter than combined head and body length 21

21. Tail less than 70 mm. and less than 65 per cent of combined head and body length; hind foot (dry, with claw) less than 25 mm.; lower first molar 3-rooted. *Phyllotis sublimis* (p. 419)

21. Tail more than 70 mm. and more than 55 per cent of combined head and body length; hind foot (dry, with claw) more or less than 25 mm.; lower molar 3- or 4-rooted 22

22. Incisors without striae or grooves; width across bullar meati one-half or more of greatest length of skull; color of upper parts of body pale; prominent ochraceous preauricular tufts present; guard hairs of rump not unusually long or conspicuously displayed; lower first molar 3-rooted. *Phyllotis boliviensis* (p. 410)

22. Incisors with weakly defined striae or grooves; width across bullar meati in fully adult individual less than one-half of greatest length of skull; upper parts of body pale; no preauricular tufts; guard hairs of rump unusually long and prominently displayed; lower first molar 4-rooted . . . *Phyllotis pictus* (p. 404)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CALOMYS SECTION
CALOMYS
ZYGODONTOMYS
ELIGMODONTIA

FIG. 27.—Distribution of the genera of the *Calomys* section of phyllotine rodents in South America and Panama. For Costa Rican portion of range see map, fig. 1.

CALOMYS SECTION

The characters of the section are given in the key (p. 118). For its geographic range, see maps (figs. 1 and 27).

Genus **CALOMYS** Waterhouse

Calomys Waterhouse, 1837, Proc. Zool. Soc. London, **1837:** 21—subgenus of *Mus* (included species: *bimaculatus* Waterhouse, type, *elegans* Waterhouse, *gracilipes* Waterhouse). Burmeister, 1854, Thiere Brasiliens, **1:** ix, 168—subgenus of *Hesperomys*, part (species: *expulsus* Lund, *lasiurus* Lund). Thomas, 1884, Proc. Zool. Soc. London, **1884:** 449—subgenus of *Hesperomys*, part (species: *bimaculatus* Waterhouse, type, *gracilipes* Waterhouse).

Hesperomys Waterhouse, 1839, Zoology Voy. "Beagle," pt. 2, no. 4, p. 75—part (*Mus bimaculatus* only). Wagner, 1843, Schreber's Säugthiere, Suppl. **3:** xii, 510—part (species: *bimaculatus* Waterhouse, *gracilipes* Waterhouse, *callosus* Rengger, *laucha* Desmarest). Baird, 1859, Mammals of North America, p. 453—part (characters, type of tribe Sigmodontes Baird). Fitzinger, 1867, Sitz. Akad. Wiss. Wien, **56,** (1), p. 26—part (species: *callosus* Rengger, *expulsus* Lund). Coues, 1874, Proc. Acad. Nat. Sci. Philadelphia, p. 177, footnote—part (*Mus bimaculatus* Waterhouse designated type). Winge, 1888, E Mus. Lundii, **3:** 11—(species: *simplex* Winge [Pleistocene], *molitor* Winge [Pleistocene], *tener* Winge, *expulsus* Lund). Thomas, 1888, Proc. Zool. Soc. London, **1888:** 133—merged with *Cricetus*. J. A. Allen, 1891, Bull. Amer. Mus. Nat. Hist., **3:** 291—"no substantial basis as a generic name." Osgood, 1909, North American Fauna, no. 28, p. 11—taxonomic history. Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17:** 141—(genus; synonym, *Calomys* Waterhouse, 1837, preoccupied [!] by *Callomys* d'Orbigny and Geoffroy 1830; species: *callosus* Rengger, *carilla* Thomas, *ducilla* Thomas, *expulsus* Lund, *gracilipes* Waterhouse, *laucha* Desmarest, *lepidus* Thomas, *sorella* Thomas, *tener* Winge, *venustus* Thomas). Tate, 1932, Amer. Mus. Nov., no. 541, p. 11—taxonomic history. Ellerman, 1941, Families and genera of living rodents, **2:** 445—part (all forms listed except *Paralomys* Thomas with *Phyllotis gerbillus* Thomas). Osgood, 1947, Jour. Mamm., **28:** 168—characters and relationships.

Eligmodontia Thomas, 1896, Proc. Zool. Soc. London, **1896:** 1020—part (*Calomys* Waterhouse and *Hesperomys* Waterhouse in synonymy).

Necromys Ameghino, 1889, Act. Acad. Nac. Ciénc., Córdoba, **6:** 110, 120—type by monotypy, *Necromys conifer* Ameghino.

Type species.—*Mus* (*Calomys*) *bimaculatus* Waterhouse, by original designation (=*Calomys laucha* Olfers).

Included species.—*Calomys laucha* Olfers, *sorellus* Thomas, *lepidus* Thomas, *callosus* Rengger.

Distribution

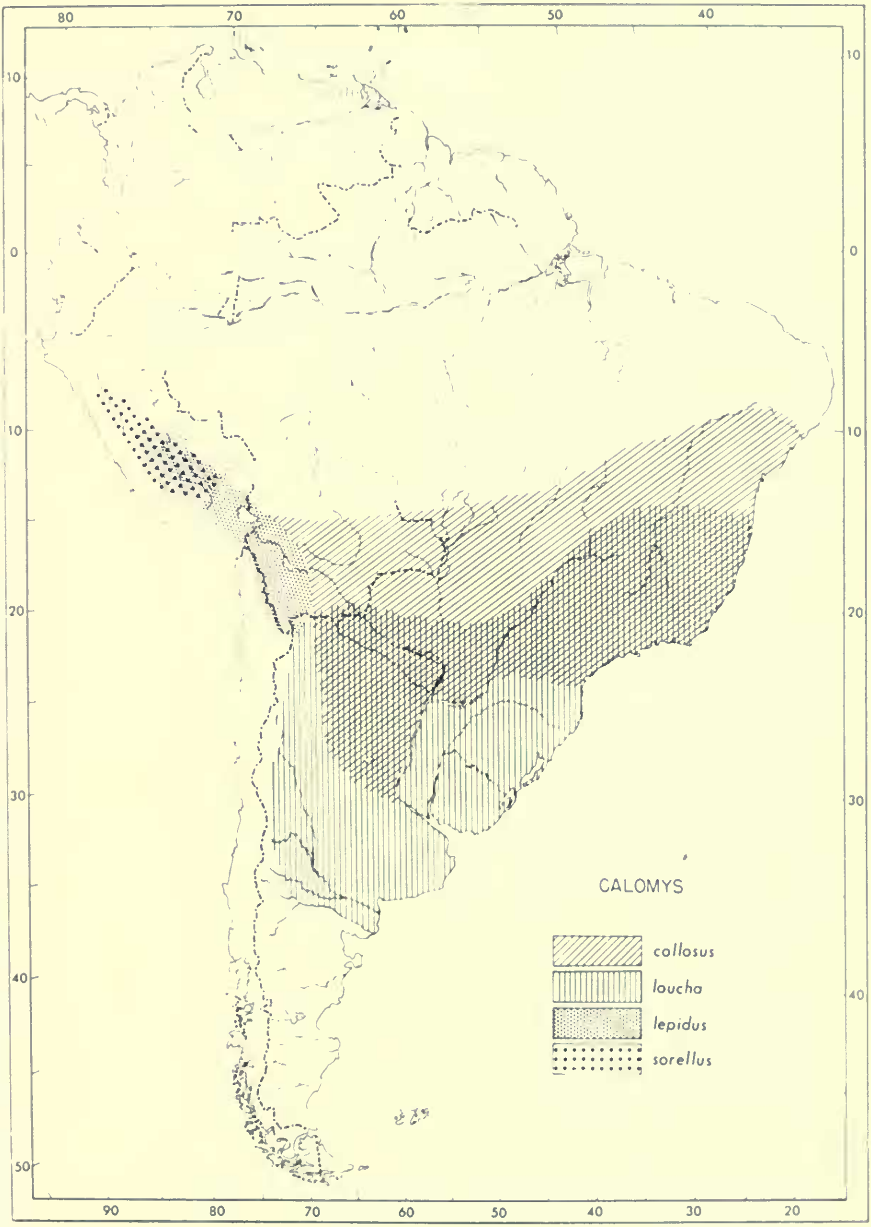
Figures 27, 28

Temperate zone grasslands, scrublands, and forest fringes of South America from the pampas of Argentina north into Paraguay, Uruguay and southeastern Brazil, west into the Andes of Peru, Bolivia and the Sierras Pampeanas of Argentina; the genus may be represented in the Bolivian Chaco and has been accidentally imported into northeastern Venezuela, Curaçao and Aruba where it is now established; altitudinal range from sea level to approximately 5000 meters above.

Characters

External.—Small, generally *Mus*-like in appearance; pelage as a rule long, thick and smoothly adpressed or moderately lax, upper parts buff or tawny to drab, under parts white to dark gray; tail usually shorter than combined head and body length, sometimes slightly longer, uniformly colored to sharply bicolor, without terminal brush; hind foot (fig. 3) small, first toe less claw not extending to base of second; fifth toe less claw not extending beyond articulation between first and second phalanges of fourth toe; plantar surface naked, with 6 small tubercles; ears small, their length from notch never more than hind foot length; postauricular tufts present or absent; mammae, 6 to 14.

Cranial (figs. 29–32).—Skull lightly built; upper surface of frontals usually convex, sometimes flat, with or without a slight median longitudinal depression; distance across mid-frontal region more or less than greatest width of rostrum; sides of supraorbital region parallel, concave or divergent, with or without beading or overhanging ledges; outline of fronto-parietal suture usually crescentic, sometimes angular; zygomatic arches little expanded, usually convergent anteriorly, rarely parallel-sided; anterior border of zygomatic plate plane or slightly concave; pitted posterolateral palatal depressions shallow or deep; paired anterior palatal pits situated on maxillaries or across maxillo-palatal sutures on anterior half of palatal bridge; width of mesopterygoid fossa at anterior base of pterygoids less than width of parapterygoid fossa measured at same plane; parapterygoid fossa shallow or moderately excavated; antero-posterior length of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CALOMYS
collosus
loucha
lepidus
sorellus

FIG. 28.—Distribution of the species of *Calomys*.

bulla (less tube) from slightly more to slightly less than length of molar row; posterior border of mandibular ramus deeply excised.

Dental (fig. 33).—Upper incisors opisthodont to nearly proodont, ungrooved; molar rows generally parallel-sided; upper first molar four-rooted, lower three- to four-rooted; $m_{\overline{3}}$ more than one-half to nearly as long as $m_{\overline{2}}$; crown crested, the cusps tuberculate, with anterior enamel walls of upper molars slightly more projecting than posterior enamel walls, and both inclined posteriorly with a slight inward rotation; principal cusps of outer side arranged in echelon or in opposition with respect to those of inner; cusps of upper molars ovate in outline, of lower ovate or tending to become triangular; anterior fold of $m^{\underline{1}}$ well developed, the procingulum distinctly bilobate in juvenal with outer conule larger than inner; mesoloph absent; an inconspicuous mesostyle sometimes present; first primary fold of $m^{\underline{2-3}}$ well developed, at least in unworn teeth; second secondary fold obsolete in upper molars; first minor fold reduced or absent in $m^{\underline{2}}$, obsolete or absent in $m^{\underline{3}}$; major fold of $m^{\underline{3}}$ sometimes coalesced with second primary fold; first internal fold sometimes, second internal fold rarely, discrete in $m^{\underline{2}}$; second internal fold of $m^{\underline{3}}$ discrete or coalesced with second primary fold; anterior fold of $m_{\overline{1}}$ present at least in unworn tooth; minor fold present in $m_{\overline{2}}$ and in unworn $m_{\overline{3}}$; second primary fold of $m_{\overline{2}}$ present, of $m_{\overline{3}}$ reduced or obsolete.

Comparisons

Small size, variable number of mammae, unspecialized hind foot, crested molars and complete absence of mesoloph are salient characters of *Calomys*. Superficial resemblance between the species of *Calomys, Mus musculus, Phyllotis amicus* and *Pseudoryzomys wavrini* is dealt with under appropriate species headings. Similarity between North American *Baiomys* and the three smaller species of *Calomys* (figs. 31–33) appears to be the result of convergence. *Baiomys* is practically inseparable from *Calomys laucha* in size, external and dental characters, and general shape of skull. It is readily distinguished, however, from all South American cricetines except *Aporodon* and *Tylomys* by its comparatively simple glans penis and bipartite baculum (cf. p. 58). It is separated from all phyllotines, including *Calomys*, by slight dorsal excision of antorbital foramen; nearly transverse, not markedly anteriorward, orientation of mediolateral axis of antorbital bridge; by postero-lateral palatal pits often wholly or partially concealed from ventral view by paired swellings on posterior border of bony palate. Characters distinguishing *Bai-*

omys from *Calomys* include the hypertrophy into a process of the burr which marks the origin of the superficialis part of the masseter muscle at root of anterior border of zygomatic process; mesopterygoid fossa always as wide as or wider than parapterygoid fossa measured at the same plane at anterior base of pterygoid processes; parapterygoid fossa shallower; fifth toe of front and hind feet longer, always extending to base of second phalanx of fourth, or slightly beyond, and pale postauricular patches absent.

Characters distinguishing *Baiomys* from *Calomys* are as trenchant as any which separate genera and supergeneric groups. Nevertheless, their small size and *Mus*-like appearance misled Husson (1960) and Packard (1960) into assuming the existence of a relationship between *Baiomys* and *Calomys* that is much closer than permitted by the facts. Husson's comparisons of *Baiomys* with *Calomys* are based on individually variable characters discussed below under the heading *Calomys laucha* (p. 143). Packard's (1960, p. 664) conclusion "on the basis of internal morphological characters studied (auditory ossicles, hyoid apparatus, and baculum) [that] *Baiomys* seems to be more closely related to a South American hesperomine [sic], perhaps *Calomys*, than to any North American cricetine" appears to be baseless. Bacula of *Baiomys* as figured by Packard (1960, p. 603) and other authors are fundamentally different from the baculum of *Calomys* and all other South American cricetines examined by me and others (cf. Hooper, 1959, p. 10). Regarding the auditory ossicles, if, as averred by Packard (1960, p. 606), those of *Baiomys* "closely resemble" those of *Calomys* and *Thaptomys* and "differ greatly" from those of *Zygodontomys*, then they must be dismissed as being devoid of taxonomic value on the generic level. *Thaptomys* is not particularly related to *Calomys* and has nothing to do with *Baiomys* while *Zygodontomys* is a phyllotine very nearly related to *Calomys*. As for the hyoid, Packard (1960, p. 603) finds that on the basis of shape "*Baiomys* seems to be most closely related to *Ochrotomys*." No comparisons were made with the hyoid of *Calomys* and no evidence is presented that the hyoid of this or any other South American rodent was examined. Packard's corollary (1960, p. 664) that "pygmy mice were more widely distributed in the past than they are at present [and that] part of the ancestral stock . . . may have emigrated from North America into South America in a brief period in the Pliocene" is entirely without foundation.

There is a striking resemblance between *Calomys callosus*, *Zygodontomys* and *Phyllotis griseoflavus* with respect to their broadly expanded supraorbital regions (fig. 34).

Variation

In all species color of head, upper parts and sides of body are *Mus*-like, under parts white to gray with or without a light buffy wash. Pale and dark color phases with intermediate stages are found in all populations. Juvenals, however, are often darker than adults. The maximum number of mammae noted in *Calomys callosus* and *C. laucha* is 14, but most females of these species show only 8. In *C. sorellus* the normal number is 8, but usually only 4 or 6 show. In *C. lepidus* there are 8 to 10 mammae, but only 6 may be detectable in the dry skin. Pale postauricular tufts are present in all species, but not in all individuals of the species. The tail is always shorter than combined head and body length in *lepidus* and *callosus* and is usually shorter or sometimes as long or slightly longer in *laucha* and *sorellus*. Hind foot is extremely variable in size. Often an "abnormally" short- or large-footed individual is found in a large series with which there is agreement in all other characters. The same is true of other size characters. An extremely large individual of an older generation than that of other individuals of the same population may appear deceptively like the sole representative of a distinct species. Conversely, a young, precociously developed individual with worn molars may be outstanding in a series of older individuals with normally developed features.

Remarks

The crested, comparatively low-crowned molars of *Calomys* are primitive phyllotine characters, but absence of the mesoloph is an advanced cricetine character. Small size, proportioned ears, variable number of mammae, and terrestrial habits are indications of the generalized cricetine pattern, but short outer toes and tendency for reduction of tail are specializations. In general, however, *Calomys* appears to be the phyllotine that has departed least from the hypothetical forest-dwelling ancestral stock.

The most generalized member of the genus is *Calomys sorellus*. *C. laucha* is practically indistinguishable but shows more than an incipient lateral expansion of the supraorbital region. This character attains maximum development in *Calomys callosus*. A parallel development of the expanded type of supraorbital region has occurred in the nearly related *Zygodontomys* and the more distant *Phyllotis griseoflavus*.

Taxonomic History

Calomys Waterhouse, 1837, is the earliest valid name for rodents hitherto referred to *Hesperomys* Waterhouse, 1839, as restricted by Thomas in 1916. The name *Calomys* fell into disuse because it was erroneously believed to be a homonym of *Callomys* d'Orbigny and Geoffroy, 1830, a genus of Chinchillidae. However, Article 56 (a) of the International Code of Zoological Nomenclature states that "even if the difference between the genus-group names is due to only one letter, these two names are not to be considered homonyms." Use of *Calomys* by Jordan (1888, p. 321) with *Hesperomys* a synonym, is as a composite of 5 North American species of cricetines, none of which was included or is now included in the *Calomys* of Waterhouse. *Calomys* Jordan, therefore, falls as a junior homonym.

Use of the name *Hesperomys* Waterhouse is one of the most embroiled in the taxonomic history of cricetines. It was proposed, in 1839, to contain all American cricetines with the same biserial molar cusp arrangement seen by Waterhouse in the teeth of the mouse he described two years earlier as *Mus* (*Calomys*) *bimaculatus.* In addition to *bimaculatus,* Waterhouse included in *Hesperomys* the species [*Peromyscus*] *leucopus, Symidon* [sic=*Sigmodon*] *hispidus,* the "species of *Neotoma,*" [*Oryzomys*] *galapagoensis,* [*Phyllotis*] *xanthopygus* and [*Phyllotis*] *darwini.* This broad, essentially supergeneric concept of *Hesperomys* was revised by Wagner (1843, p. 510) to include the South American *Scapteromys, Oxymycterus, Abrothrix* and *Calomys,* all described by Waterhouse in 1837 as subgenera of *Mus.* Wagner, and after him Burmeister (1854, p. ix), continued to employ *Hesperomys* as a "supergenus" of South American cricetines. The literature of purely North American cricetines also became involved with *Hesperomys.* Baird (1859, p. 453) made it type of the tribe *Sigmodontes* (=*Cricetinae* of modern authors) and referred 10 species, now included in *Peromyscus,* to the genus *Hesperomys.* Still no genotype was designated, but one of the 10 species mentioned, *leucopus,* was also included by Waterhouse in the original definition of *Hesperomys.* Finally, Coues (1874, p. 177), pointed out that "Waterhouse, in drawing his comparison between *Mus* and the New World mice, took *M. rattus* and *M. bimaculatus* for such purpose; we may properly therefore elect the latter as technically the type." This statement is the first clear and unequivocal determination of the status of *Hesperomys.* The name, therefore, by virtue of its designated genotype, is an absolute synonym of *Calomys* Waterhouse.

Hesperomys of Winge (1887, p. 11) is equivalent to *Calomys* as defined here, while his *Calomys* is the *Oryzomys* of modern literature. Winge distinguished *Hesperomys* from his *Calomys* (=*Oryzomys*) by the presence of a well-developed mesoloph in the molars of the latter and its absence in those of the former. He also observed that the molars of *Hesperomys* and *Cricetus* were similar in this respect. Thomas (1888, p. 133) went farther and proposed that the name *Hesperomys* "be abolished altogether and [its] species united with the Old-World Hamsters under the name *Cricetus*." J. A. Allen (1891, p. 291) also voted for the elimination of *Hesperomys* as an invalid name, but he objected to the transfer of its species to *Cricetus*. Thomas (1896, p. 1020) compromised by sinking both *Hesperomys* and *Calomys* in the synonymy of *Eligmodontia* Cuvier. This solution endured until 1916, when Thomas (1916a, p. 141) revived *Hesperomys* (instead of *Calomys*, supposedly invalidated by *Callomys* d'Orbigny and I. Geoffroy), as the generic name for *lauchas*.

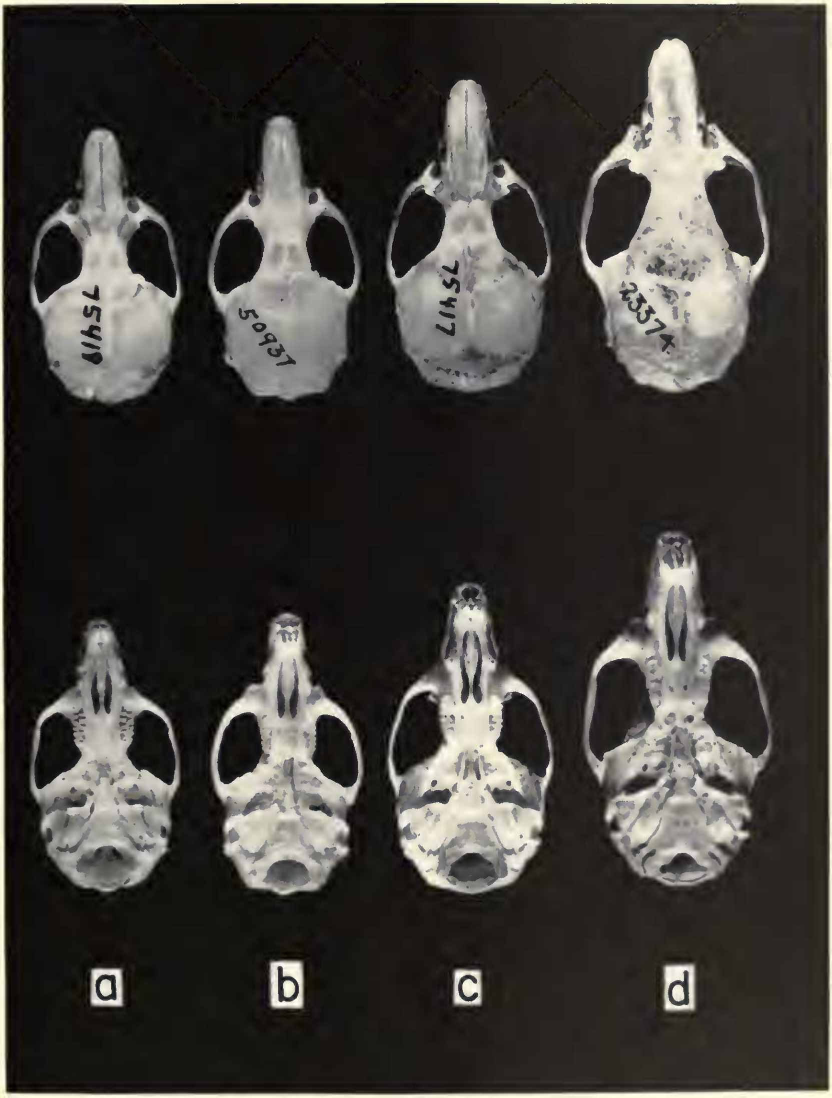
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FIG. 29. — Dorsal and palatal aspects of skulls of *a*, *Calomys lepidus lepidus*; *b*, *C. laucha laucha*; *c*, *C. sorellus*; *d*, *C. callosus callosus*. (Enlarged.)

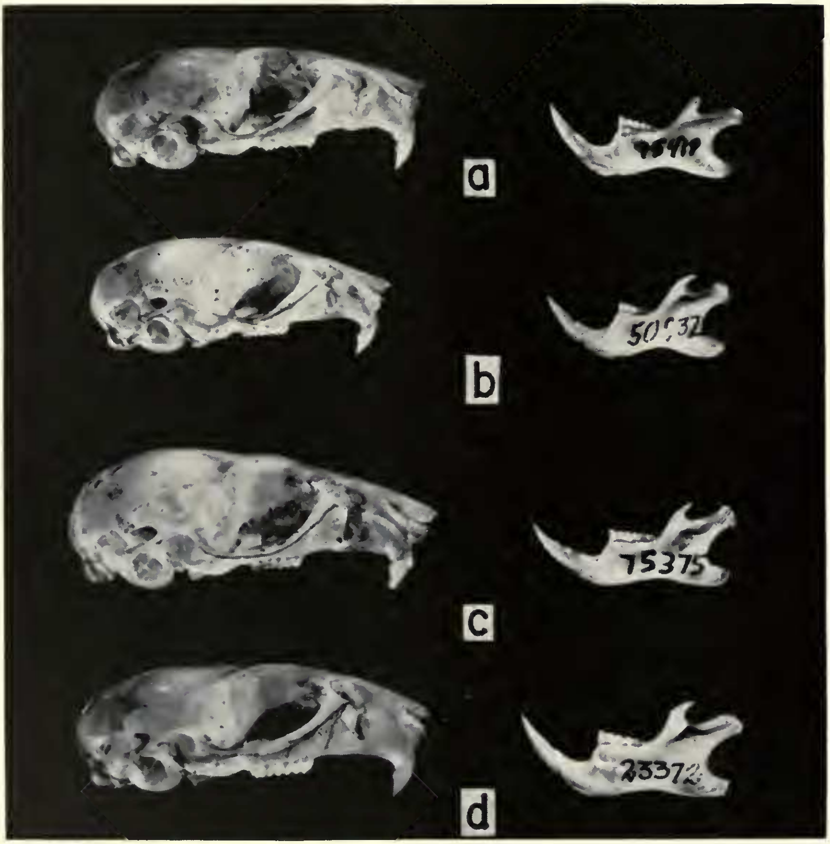
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FIG. 30.—Side view of skull and outer surface of mandible of *a*, *Calomys lepidus lepidus*; *b*, *C. laucha*; *c*, *C. sorellus*; *d*, *C. callosus callosus*. (Enlarged.)

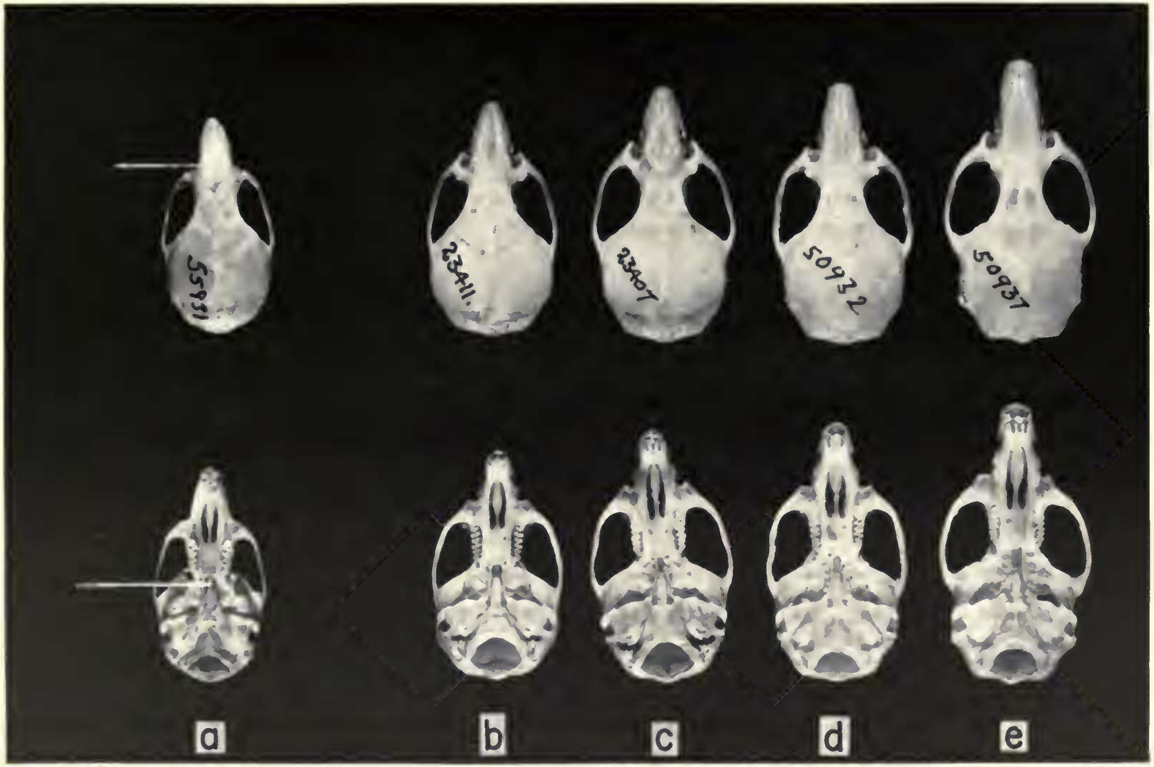
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FIG. 31.—Dorsal and palatal aspects of skulls of *a*, *Baiomys taylori*; *b–e*, *Calomys laucha*, juvenal to old adult. Note fully functional molars of juvenal (*b*). (Enlarged.)

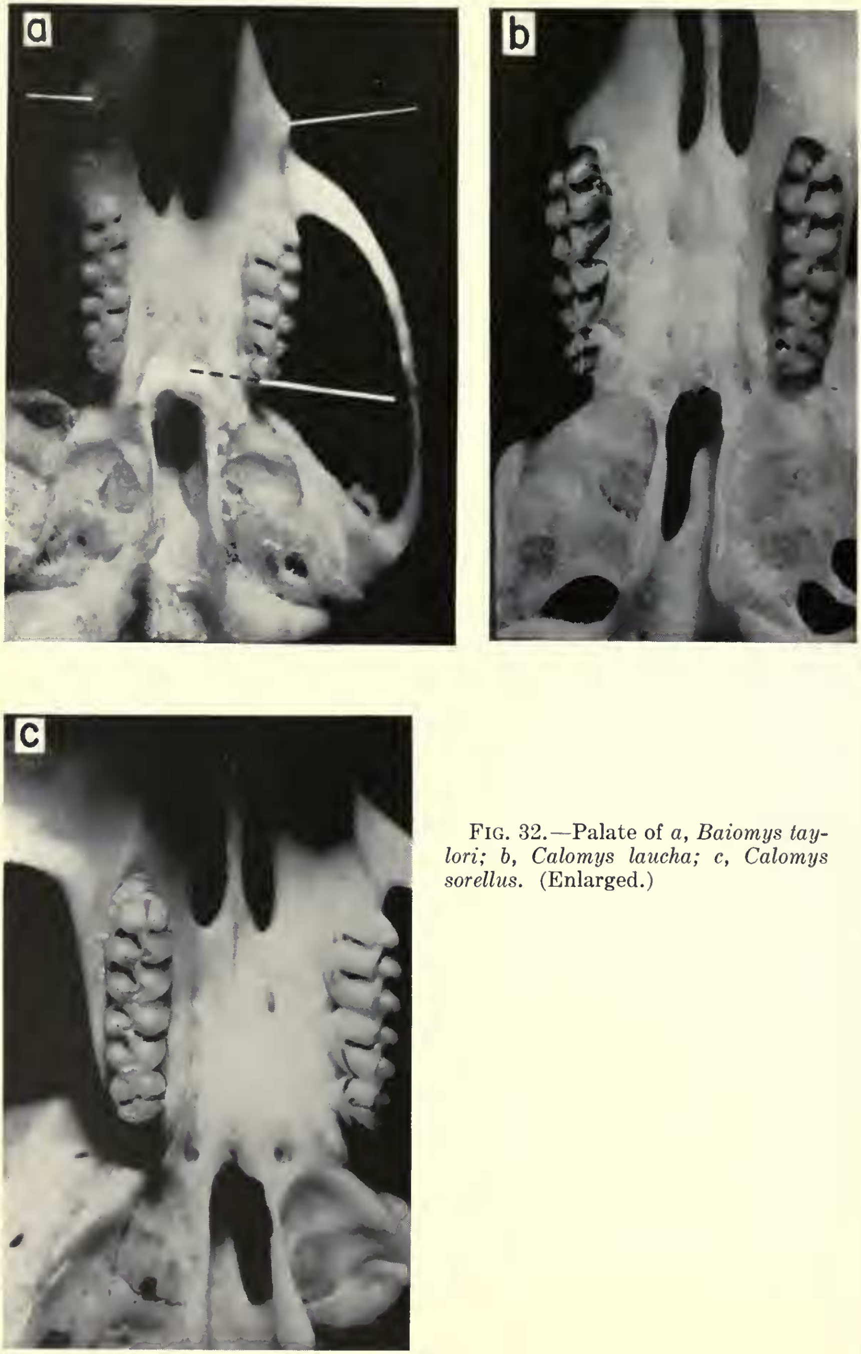

FIG. 32.—Palate of *a*, *Baiomys taylori*; *b*, *Calomys laucha*; *c*, *Calomys sorellus*. (Enlarged.)

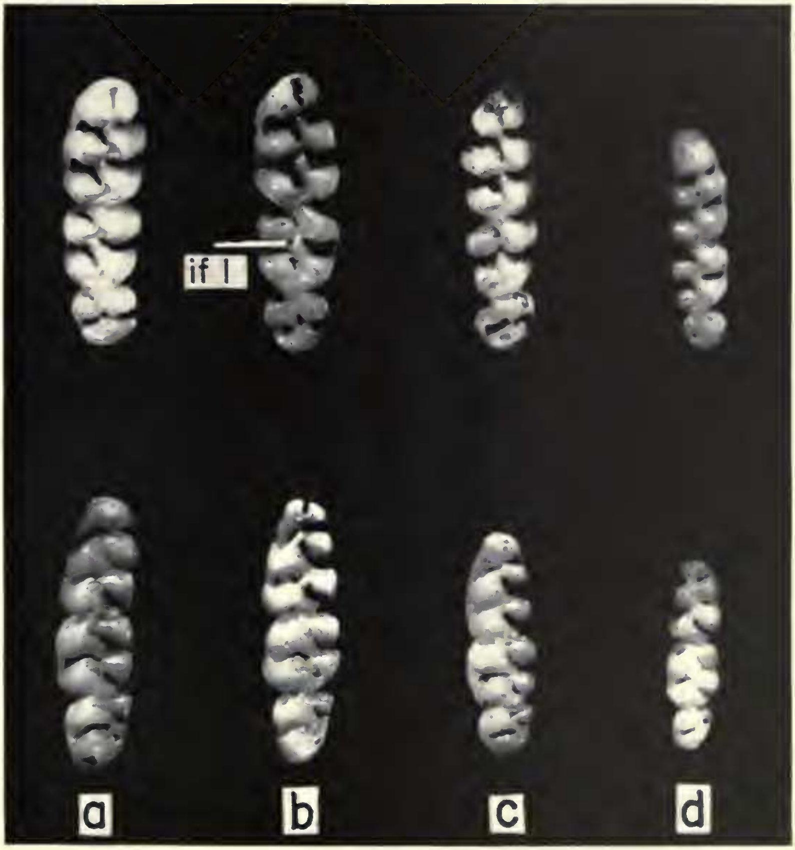

FIG. 33.—Right upper molars and lower left molars of *a*, *Calomys sorellus*; *b*, *C. laucha*; *c*, *C. lepidus*; *d*, *Baiomys taylori*. (Enlarged.)

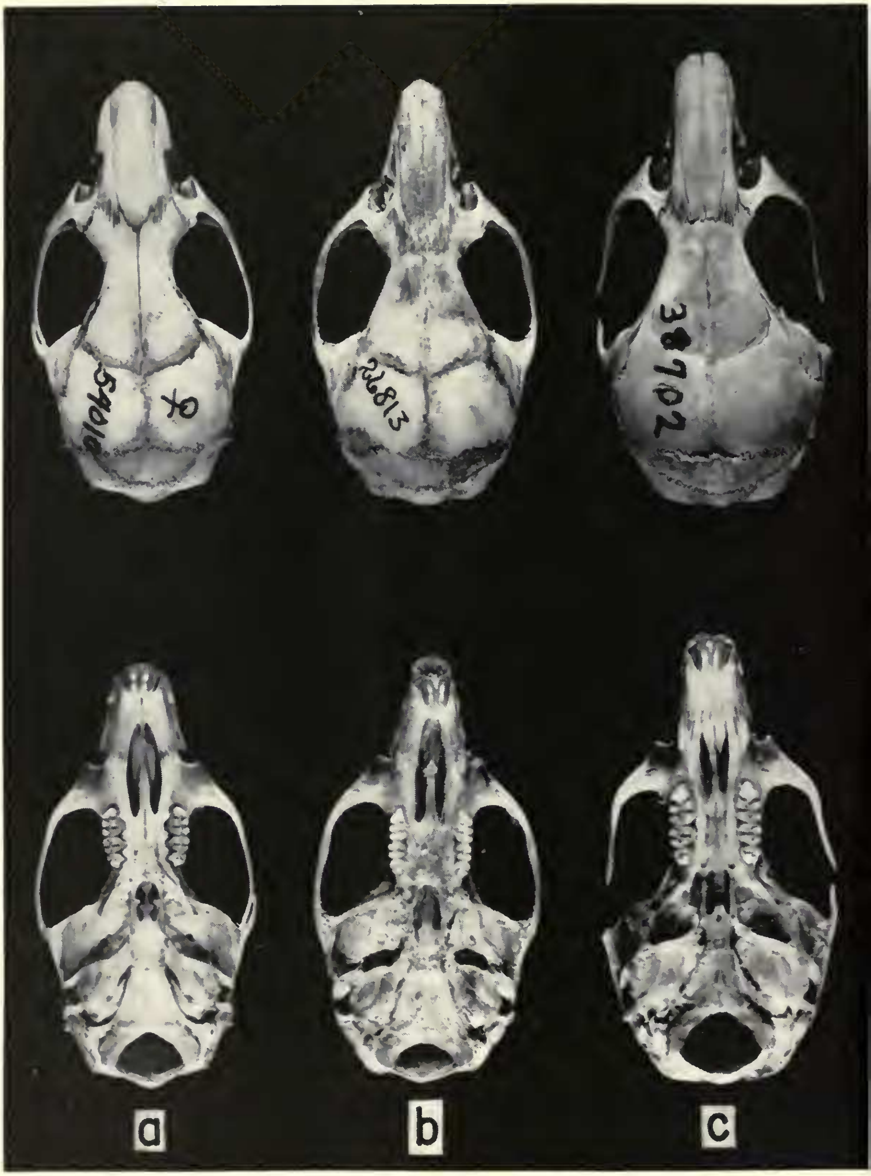
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FIG. 34.—Dorsal and palatal aspects of skulls of *a*, *Zygodontomys brevicauda*; *b*, *Calomys callosus*; *c*, *Phyllotis griseoflavus*. (Enlarged.)

DIAGNOSTIC CHARACTERS AND KEY TO THE SPECIES OF *CALOMYS*

1. Borders of supraorbital region of skull divergent from front to back, strongly beaded and forming broad ledges in fully mature individuals; mid-frontal width always more than greatest width of rostrum; interparietal usually well developed antero-posteriorly; greatest length of adult skull at least 24 mm.; alveolar length of molar row 4.0 mm. or more; head and body length more than 80 mm., tail more than 60 mm. . . . .*callosus*

1. Borders of supraorbital region parallel, divergent or slightly concave mid-frontally, the edges square, never beaded and never forming ledges except, sometimes, in very old individuals; mid-frontal width more or less than greatest width of rostrum; interparietal usually narrow antero-posteriorly; greatest length of skull less than 26.5 mm.; alveolar length of molar row less than 4.3 mm.; head and body more or less than 80 mm., tail more or less than 60 mm. . .2

2. Tail less than 50 mm. long, whitish or pale gray; heel and proximal portion of soles covered with hair, the tarsal tubercle partially hidden from view; sides of supraorbital region of skull parallel or very slightly concave mid-frontally and never forming ledges; mid-frontal width less than greatest width of rostrum; posterior tip of lower incisor indicated as a ridge without capsular projection on outer side of mandible. . . . .*lepidus*

2. Tail more than 30 mm. long, brown above, paler beneath; heel, only, covered with hair; sides of supraorbital region of skull divergent or parallel, the edges square or tending to form ledges in old individuals; mid-frontal width more or less than greatest width of rostrum; posterior tip of lower incisor encased in projecting capsule. 3

3. Supraorbital borders usually parallel or slightly divergent mid-frontally, the edges never forming ledges; mid-frontal width equal to or less than greatest width of rostrum; habitat Peru. . . . .*sorellus*

3. Supraorbital borders usually divergent throughout their length except at extreme anterior portions, the edges tending to form ledges in old individuals; mid-frontal width equal to or more than greatest width of rostrum . . . .*laucha*

Calomys sorellus Thomas

Eligmodontia sorella Thomas, 1900, Ann. Mag. Nat. Hist., (7), **6**: 297. Osgood, 1914, Field Mus. Nat. Hist., Zool. Ser., **10**: 166—PERU: *La Libertad* (mountains northeast of Otusco).

[*Hesperomys*] *sorella*, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 141—classification.

Hesperomys sorella, Pearson, 1957, Breviora, Mus. Comp. Zool., no. 73, p. 1—PERU: *Puno* (3 miles northeast of Arapa; 5 miles south of Asillo; Hacienda Calacala, 7 miles southwest of Putina).

Calomys lepidus sorellus, Cabrera, 1961, Rev. Mus. argentino Cienc. Nat., "Bernardino Rivadavia," **4**: 481—classification.

Hesperomys frida Thomas, 1917, Smithsonian Misc. Coll., **68**, no. 4, p. 1—PERU: *Cusco* (type locality, Chospioc). Thomas, 1920, Proc. U. S. Nat. Mus., **58**: 230, pl. 14, fig. 3 (skull)—PERU: *Cusco* (Huaracondo; Chospioc; Torontoy; Querefrata; Anta).

Calomys frida frida, Cabrera, 1961, Rev. Mus. argentino Cienc. Nat., "Bernardino Rivadavia," **4**: 478—classification.

Hesperomys frida miurus Thomas, 1926, Ann. Mag. Nat. Hist., (9), **17**: 314—PERU: *Junín* (type locality, Yana Mayo, Río Tarma). Thomas, 1927, op. cit., (9), **20**: 602—PERU: *Pasco* (Huariaca; Alcas).

EXPLANATION OF FIGURE 35

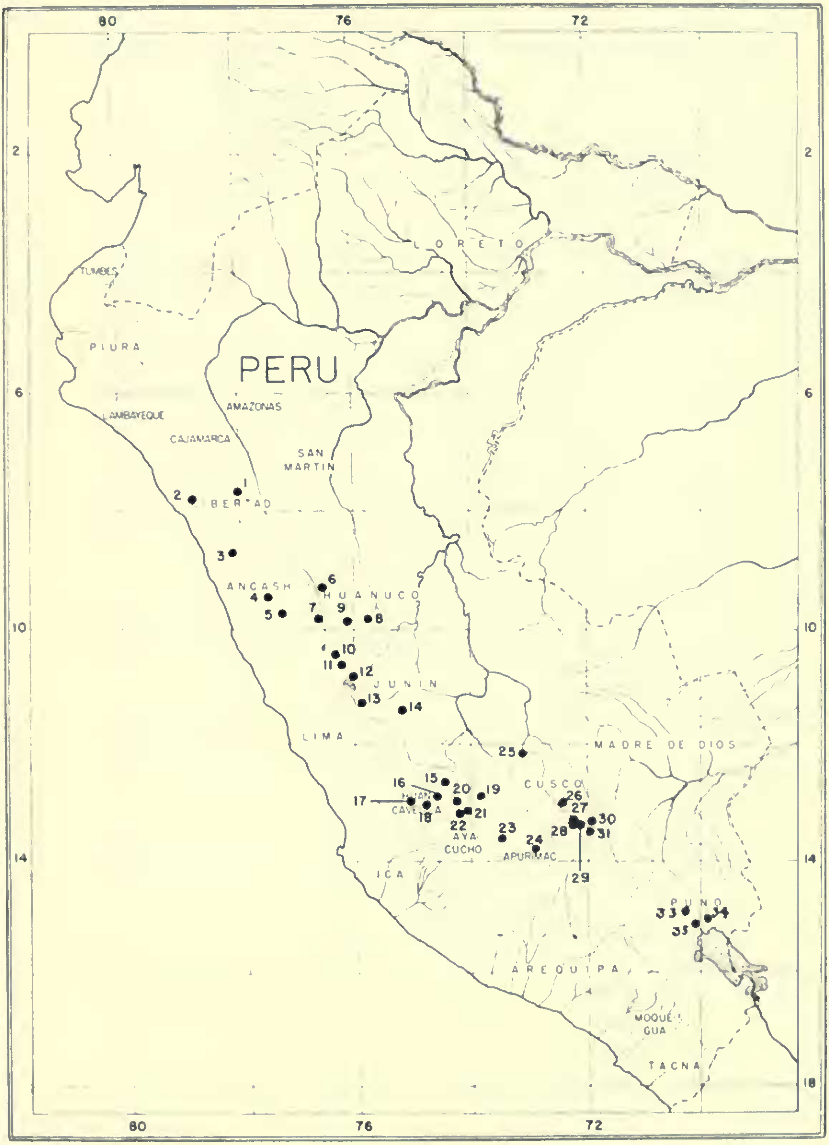
Calomys sorellus: collecting localities and collectors.

Type localities in **boldface.**

Calomys sorellus (1–35)

PERU

1. **Huamachuco, 8 miles south, La Libertad.**—P. O. Simons.
2. Otuzco, mountains northeast of, La Libertad.—W. H. Osgood and M. P. Anderson at 10,000 feet.
3. Macate, Ancash.—W. H. Osgood and M. P. Anderson.
4. Tullparaju, Huaraz, Ancash.—C. Kalinowski at 4300 meters.
4. Quilcayhuanca, Huaraz, Ancash.—C. Kalinowski at 4000 meters.
5. Catac (Hacienda), Ticapampa, Ancash.—C. Kalinowski at 3500 meters.
6. Cullcui, Río Marañon, Huánuco.—J. T. Zimmer at 10,400 feet.
7. Huánuco Viejo, Huánuco.—J. T. Zimmer at 12,700 feet.
8. Panao Mountains, Huánuco.—J. T. Zimmer at 10,300 feet.
9. Huánuco, Huánuco.—J. T. Zimmer at 12,200 feet.
10. Alcas, Huariaca, Pasco.—R. W. Hendee at 11,500 feet.
10. Huariaca, Pasco.—R. W. Hendee at 9000 feet.
11. La Quinua, Pasco.—E. Heller at 11,600 feet.
12. Carhuamayo, Junín.—C. C. Sanborn at 14,500 feet.
13. La Oroya, Junín.—M. P. Anderson at 12,000 feet.
14. **Yana Mayo, Río Tarma, Junín.**—Type locality of *miurus*; R. W. Hendee at 8500 feet.
15. Piso (Hacienda), Locroja, Huancavelica.—C. Kalinowski.
16. Mayoc, Locrojo, Huancavelica.—C. Kalinowski.
17. Huancavelica, Huancavelica.—C. Kalinowski at 3680 meters; A. R. G. Morrison at 12,000 feet.
18. Lircay, Huancavelica.—C. Kalinowski at 3310 meters.
19. Tambo, San Miguel, Ayacucho.—C. Kalinowski.
20. Huanta, Ayacucho.—C. Kalinowski.
21. Puente Pajonal, Ocros, Ayacucho.—C. Kalinowski at 1900 meters; includes Hacienda Pajonal, 1900 meters.
22. Ocros, Ayacucho.—C. Kalinowski at 3150 meters.
23. Andahuaylas, Apurimac.—C. Kalinowski; locality includes Hacienda Mozabamba, 2300 meters; Hacienda Palmar, 2200 meters; Uripa, 3100 meters; Hacienda La Laguna, 3040 meters.
24. Quebrada Matara, Apurimac.—C. C. Sanborn; includes Hacienda La Victoria, 7000 feet; Hacienda Matara, 6200 feet.
25. Chirapata, Cosireni Pass, Cuzco.—E. Heller.
26. Torontoy, Cuzco.—E. Heller at 12,000 feet.
27. **Chospioc, Cuzco.**—Type locality of *frida;* E. Heller at 10,000 feet.
28. Huaracondo, Cuzco.—E. Heller at 10,850 feet.
29. Anta, Cuzco.—O. Garlepp.
30. Urco (Hacienda), near Calca.—J. M. Schmidt at 9500–10,000 feet.
31. Cuzco, Cuzco.—C. C. Sanborn.
32. Querefrata, Cuzco.—Not located; E. Heller.
33. Arapa, 3 miles northeast, Puno.—O. P. Pearson at 12,600 feet.
34. Asillo, 5 miles south, Puno.—O. P. Pearson at 13,000 feet.
35. Calacala (Hacienda), 7 miles southwest of Putina.—O. P. Pearson at 13,000 feet.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ANCASH
HUANUCO
JUNIN
LIMA
HUANCAVELICA
AYACUCHO
APURIMAC
CUSCO
MADRE DE DIOS
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AREQUIPA
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FIG. 35. Collecting localities of *Calomys sorellus*. See opposite page for explanation.

Type.—Female, British Museum (Natural History) no. 0.6.6.29; collected November 28, 1899, by Perry O. Simons.

Type locality.—Eight miles south of Huamachuco, La Libertad, Peru; altitude, 3500 meters above sea level.

Distribution (fig. 35).—Peruvian Andes from the department of La Libertad southward into Cusco and Puno. Altitudinal range from approximately 2000 to 4600 meters above sea level.

Characters.—Larger of the two known Peruvian species of *Calomys;* pelage long, soft, moderately lax, underfur thick; tail from approximately 60 per cent to fully as long as head and body combined, exceptionally slightly longer; tail bicolor except, often, at extreme tip; fifth hind toe long but not extending beyond articulation between first and second phalanges of fourth toe; white or buffy postauricular tufts present but not always conspicuous; upper parts of body ochraceous to tawny mixed with black; a more or less defined, sometimes broken, ochraceous lateral line present; tip of muzzle usually ochraceous; under parts gray, rarely with a weak buffy wash; mammae normally 8, but usually only 4 or 6 detectable in dry skin; borders of supraorbital region of skull (figs. 29, 30, 36) slightly divergent, the edges square, never beaded; mid-frontal width about equal to or, usually, less than greatest width of rostrum; interparietal extremely reduced antero-posteriorly; other external and cranial characters as given in the key (p. 137); dental characters (figs. 32, 33) as for the genus.

Comparisons.—*Calomys sorellus* is distinguished from the allopatric *C. laucha* chiefly by larger average size, fifth hind toe slightly longer, sides of supraorbital region less divergent, their edges less sharply squared. Comparison with the partially sympatric *C. lepidus* is made elsewhere (p. 160). The superficial resemblance between *C. sorellus* and *Phyllotis amicus* is restricted to character of pelage, color, and small body size.

Variation.—A tawny and a dark, or olivaceous, phase are present in most series. Individuals may molt from one phase to the other. The molt cycle is individual rather than seasonal in present material. A gradient or other pattern of geographic variation in color or size is not evident.

Taxonomy.—Specimens from northeast of Otuzco, La Libertad, here regarded as most nearly representing the type of *sorellus* Thomas, were identified as such by Osgood (supra cit.). Evidently this species was overlooked by Thomas when he described one of

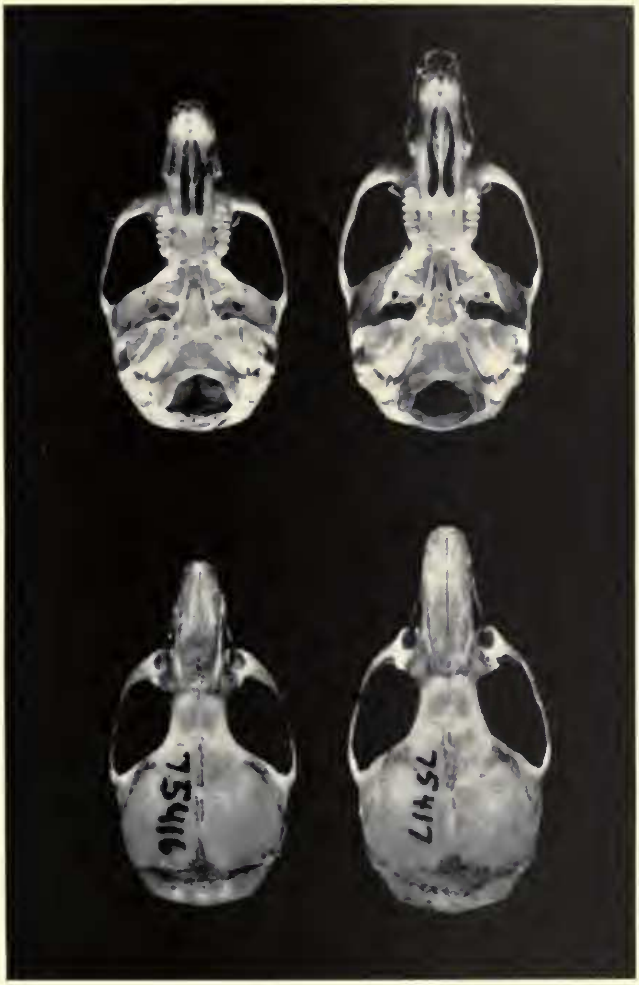


FIG. 36. *Calomys sorellus.* Dorsal and ventral aspects of skulls of two adults from Lircay, Peru. (× 2.)

its representatives from southern Peru under the new name *Hesperomys frida.* It was compared with *Phyllotis,* and some differences between *Calomys frida* and *callosus* ("*H. venustus*") were noted. *Calomys sorellus* was again ignored when Thomas erected *Hesperomys frida miurus.* This was characterized as shorter-tailed than typical *frida.* Tail measurements of *miurus* and *frida* are given below, following their respective combined head and body measurements:

miurus: head and body, 86; tail, 76; tails of additional specimens, 70–80 mm.

frida: head and body, 102; tail, 91; tails of additional specimens, 82, 85, 85, 87 mm.

The measurements reveal that the tail of the type of *miurus* is approximately 47 per cent of total length and that of *frida* is also about 47 per cent of total length. Furthermore, the tail length of *miurus* is approximately average for the series to which it belongs, while that of the type of *frida* is extremely long.

Habits and habitat.—The two specimens recorded by Osgood from the northern Peruvian Andes northeast of Otuzco, at 11,000 feet above sea level, "were caught in tall grass and weeds growing about the base of rough limestone exposures on the very top of the mountains." This is all that is known of the life history of *Calomys sorellus.*

Measurements.—See Table 2 (p. 189).

Specimens examined.—130, all in collection of Chicago Natural History Museum. PERU.—*La Libertad:* Otuzco, 2. *Ancash:* Macate, 1; Hacienda Catac, Ticapampa, Tullparaju, Huaraz, 2; Quilcayhuanca, Huaraz, 2. *Huánuco:* "Panao Mountains," 3; Huánuco, 8; Huánuco Viejo, 1; Cullcui, Río Marañon, 1. *Pasco:* Quinua, 9. *Junín:* Yana Mayo, 1; Oroya, 2; Carhuamayo, 1. *Huancavelica:* Hacienda Piso, Locroja, 3; Mayoc, Locroja, 1; Huancavelica, 15: Lircay, 11. *Ayacucho:* Tambo, San Miguel, 10; Huanta, 4; Ocros, 4; Puente Pajonal, Ocros, 3. *Apurimac:* Andahuaylas, 16; Quebrada Matara, 9. *Cusco:* Chirapata, Cosireni Pass, 1; Hacienda Urco, near Calca, 15; Cusco, 5.

Calomys laucha Olfers. (Synonymy under subspecies.)

Distribution (maps, figures 28 and 37).—Grasslands and scrublands in southern Minas Geraes, south through the Brazilian coastal states into Paraguay, Uruguay and the Sierras Pampeanas and plains of Argentina as far as the Río Negro; west to the Andean foothills of extreme southern Bolivia; established as import colonies in Monagas, Venezuela, and the Netherlands West Indian islands of Curaçao and Aruba; altitudinal range from sea level to approximately 2500 meters above.

Characters.—Smallest phyllotine within its geographic range; pelage long, thick, smoothly adpressed; tail from approximately 35 per cent to 108 per cent of combined head and body length, brownish above, beneath paler but never sharply defined white; fifth hind toe, less claw, not extending to tip of first phalanx of fourth toe (fig. 38); pale buff to white postauricular patches usually present; upper parts of body buff to tawny finely mixed with black; an ochraceous lateral line often present; under parts of body from sharply defined white to moderately well-defined grayish with or without an ochraceous wash, base of hairs of belly and chest slaty; mammae from 8 to 14; borders of supraorbital region of skull (figs. 29-31) divergent, the edges square, never beaded; mid-frontal width equal to or more than greatest width of rostrum; interparietal usually narrow anteroposteriorly. Other external and cranial characters as given in the key (p. 137); dental characters (figs. 32, 33) as for the genus.

Comparisons.—Remarkable resemblances between the nonphyllotine *Baiomys* and *Calomys laucha* have been discussed under the generic heading (p. 127 and figs. 31, 32). Characters used by Husson (1960, p. 38) for distinguishing the two genera are variable and confused. This author compared his six specimens of "*Baiomys*" *hummelincki* (=*Calomys laucha*) with four of the same species from Argentina, one specimen of *C. lepidus* from Peru, two of *Baiomys taylori* from Texas and four of *B. musculus* from México. He concluded that *Baiomys* differed from *Calomys laucha* by its smaller, more rounded m^3, with major fold obsolete or absent, and by the shape of its interparietal, which was said to be broader anteroposteriorly and shorter transversely, extending only about one-half the distance across the braincase. In the approximately 100 Chicago Natural History Museum specimens of *Baiomys* represented by *B. taylori* and *B. musculus*, m^3 is often, if not usually, smaller and more rounded in outline than in most comparable specimens of *Calomys laucha*. The third molar of the latter, however, is so variable in size and shape that all conditions found in *Baiomys* are frequently duplicated in *Calomys*. Unworn m^3 of *Calomys laucha* is usually indistinguishable from worn or unworn m^3 of *Baiomys*. The major fold is usually open to the margin in *Calomys* but sometimes appears only as an enamel island, quite as in "*Baiomys*" *hummelincki*. In *Baiomys musculus* the major fold is usually an enamel island, the marginal flexure being obsolete or absent. In contrast, the major fold of m^3 in *B. taylori* is open at the margin in nearly all but the most worn teeth. Packard's (1960, p. 586) figures of the enamel pattern of the molars of *Baiomys* are not clear on this matter. His figure of m^3 in *B. taylori* lacks the marginal flexure or any other indication of the presence of the major fold, while that of *B. musculus* shows a weak marginal flexure. Variation in the structure of the

EXPLANATION OF FIGURE 37

Calomys laucha: collecting localities and collectors. Type localities in **boldface.**

Calomys laucha tener (1–2)

BRAZIL (1–2)

1. **Rio das Velhas, Lagôa Santa, Minas Geraes.**
2. Piracicaba, São Paulo.

Calomys laucha laucha (3–37)

BOLIVIA (3–4)

3. Tablada, Tarija.—E. Budin at 2000 meters.
4. Sama, Tarija.—E. Budin at 4000 meters.

PARAGUAY (5–8)

5. Guachalla, Chaco.—P. Willem.
6. Orloff, Chaco.—Y. Unger.
7. **Asunción.**—F. Azara.
8. Aguairenda, Chaco.—not located and not shown on map.

URUGUAY (9–11)

9. Paso de los Averías, Río Cebollati, Minas.—C. C. Sanborn.
10. Polanco, Minas.—C. C. Sanborn.
11. Maldonado.—C. Darwin.

ARGENTINA (12–34)

12. Santa Catalina, Jujuy (3802 meters).—E. Budin at 4500 meters.
13. Maimará, Jujuy.—E. Budin.
14. Jujuy, Jujuy.—E. Budin at 2230 meters.
15. Tala, Salta (=Río Tala, Tucumán near Salta border?).—Borelli.
16. Ñorco (=Ñorco Simbolán), Tucumán.—E. Budin at 1500–2000 meters.
17. Concepción, Tucumán.—J. Mogensen at 400–500 meters.
18. La Puntilla, near Tinogasta, Catamarca.—E. Budin.
19. Chumbicha, Catamarca (415 meters).—E. Budin at 600 meters.
20. Goya, Corrientes.—R. Perrens.
21. Yacanto, near Villa Dolores, Córdoba.—R. Kemp at 900–1000 meters.
22. Cañada Honda, San Juán.—E. Budin at 500 meters.
23. Buenos Aires, Buenos Aires.
24. La Plata, Buenos Aires.—O. Thomas.
24. Ensenada, Buenos Aires.—C. Spegazzini; O. Thomas.
25. San Miguel, Buenos Aires.—J. Crespo.
26. Henderson, Buenos Aires.—W. H. Osgood.
27. Torrecito, Buenos Aires.—W. H. Osgood.
28. Los Inglesas, Buenos Aires.—H. E. Box.
29. Dorrego (=Coronel Dorrego), 10 km. northwest, Buenos Aires (113 meters).—C. C. Sanborn.
30. Bahía Blanca, Buenos Aires.—O. Thomas.
31. Algarrobo, Buenos Aires (47 meters).—J. Yepes.
32. Pichi Mahuida, La Pampa (119 meters).—E. Budin at 650 meters.
33. Chimpay, Río Negro (170 meters).—C. C. Sanborn.
34. Choele-Choel, Río Negro.—E. Budin.

NETHERLANDS WEST INDIES (35–36)

35. Curaçao.—A. B. Bitter; P. Wagenaar Hummelinck Collection.
36. Aruba.—P. Wagenaar Hummelinck; A. D. Ringma.

VENEZUELA (37)

37. Maturín, 42 km. south, Monagas.—B. B. Butterworth.

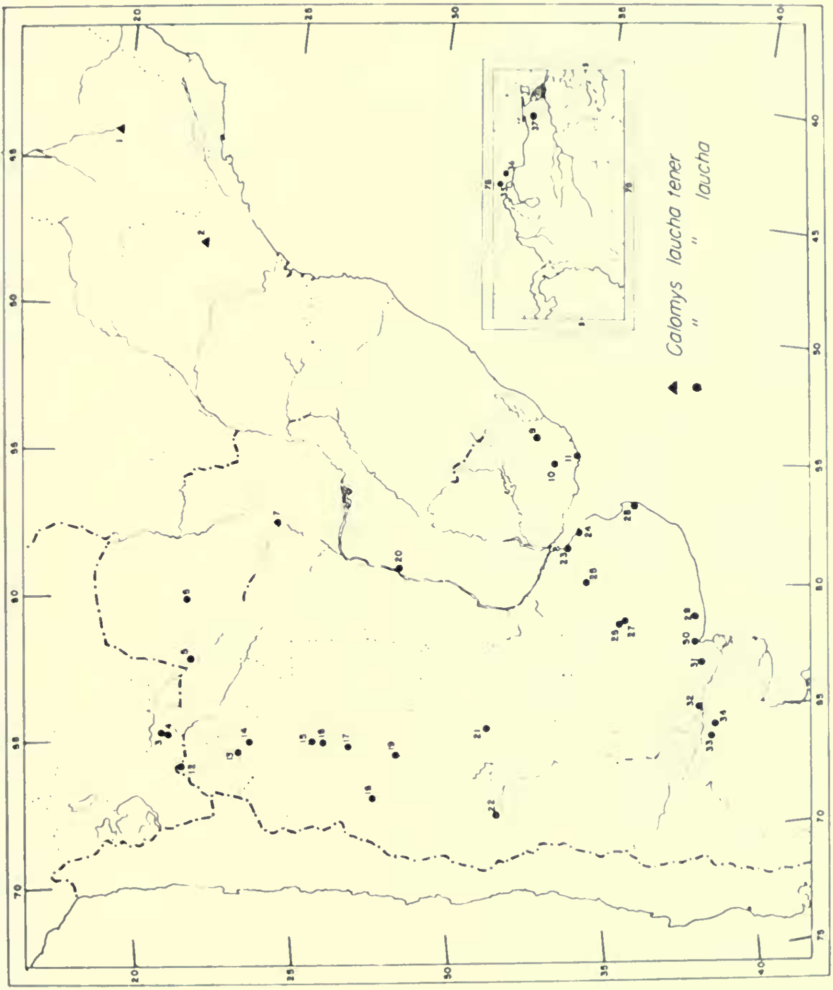

▲ Calomys laucha tener
● " laucha
20
25
30
35
40
45
50
55
60
65
70
75

FIG. 37.—Collecting localities of the subspecies of *Calomys laucha*. See opposite page for explanation.

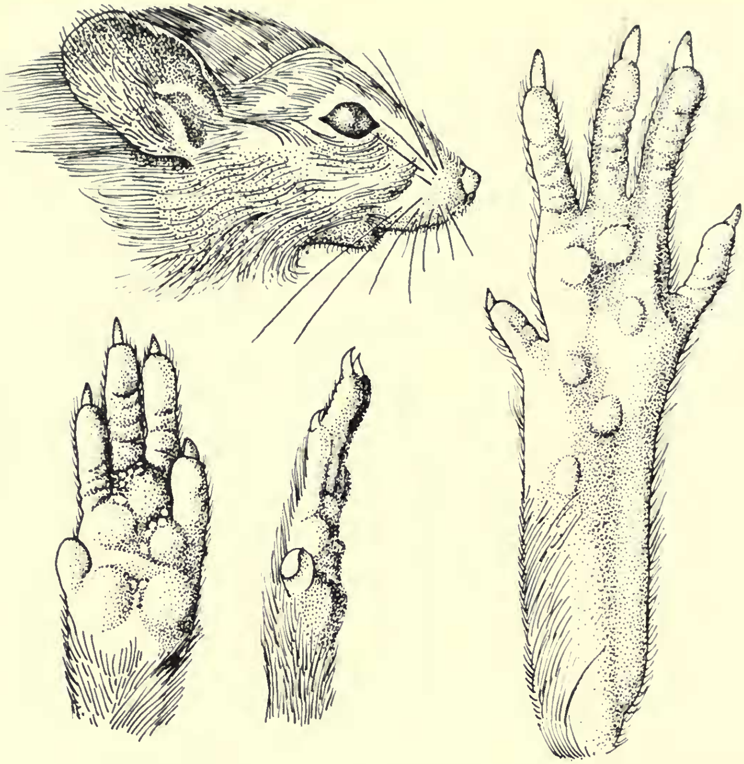


FIG. 38.—*Calomys laucha.* Head, fore and hind feet of specimen preserved in alcohol. Copied from the original drawings of *Baiomys hummelincki* Husson (1960, fig. 7).

third molar in cricetines in general and its significance in dental evolution is discussed elsewhere (p. 100). Regarding Husson's interparietal character, the bone extends nearly or quite across the width of the two parietals combined in *Calomys laucha* including three skulls at hand of the original series of *"Baiomys" hummelincki,* and in *Baiomys musculus.* In *B. taylori* the interparietal usually extends only two-thirds the distance, sometimes the full distance, across both interparietals.

The introduced *Mus musculus,* often found together with *Calomys* in houses and surrounding grounds, is also similar in superficial characters and in general outline of skull. *Mus* and *Calomys* also agree in size, relative length of tail, limb proportions and number of mammae. In *Mus musculus,* however, pelage is comparatively shorter, thinner and usually unctuous; under parts darker, washed with ochraceous and little or not at all defined from sides; lateral line absent; tail often monocolor; hairs of upper surface of hands and feet dark; post-auricular patches absent. Differences between *Mus* and *Calomys* in details of cranial structure and enamel pattern of molars are obvious and need not be discussed here.

Nearest *Calomys laucha* is the allopatric *C. sorellus*, known only from Peru. Proper appraisal of the slight differences between the two cannot be made without knowledge of whether or not either or both forms occur in the intervening highlands of Bolivia.

Where *Calomys laucha* and *C. callosus* are found together the latter is larger throughout, with distinctive cranial characters. Very old individuals of *C. laucha*, however, approach and may equal in size young adults of *C. callosus*. In these cases, the alveolar length of the molar row of the first species is less than that of the second.

Variation.—Size differences between adults of any one population are more remarkable than average size differences between populations. Evidently *lauchas* attain maturity within a few weeks after birth, but their growth continues throughout a life span of months and, potentially if not actually, of years. Old pelage is more gray than new and molt seems to follow a seasonal pattern, as shown by the following specimens from Uruguay and eastern Argentina.

No. of specimens	Locality	Date	Condition of pelage
2	Minas, Uruguay	Nov. 21–23	molting
2	Algarrobo, Buenos Aires	Jan., 1926	worn
7	Near Dorrego, Buenos Aires	April 2–3, 1940	molting
7	Chimpay, Río Negro	April 6–7, 1940	molting
2	Choele-Choel, Río Negro	May, 1928	new
12	Torrecita, Buenos Aires	May 30–June 2, 1923	new

It appears that old pelage coincides with summer, new pelage with winter; spring and fall are molt periods.

Geographic variation, if present in the species, is masked in present material by individual variation in size, age differences, and seasonal differences in color and pelage.

Habits and habitat.—The *laucha* is the common pampa mouse. Its name is the one applied by natives to any small rodent and Azara adopted it for *Calomys* for want of another. The *laucha* lives in grass clumps, among cacti, in piles of rock, rubbish, weeds, and faggots, and in and about houses. Charles Darwin (*in* Waterhouse, 1839, p. 44) noted that the peasant who brought him the type of *Calomys bimaculatus* found six of the same species "living together in one burrow." On the other hand, Oldfield Thomas

(1916b, p. 184) made other observations during his collecting trip into the La Plata region in 1896. "This animal [i.e., *Hesperomys murillus*, which Thomas thought was different from true *H. laucha*] is not much of a burrower, but lives about in the grass, and examples may be easily obtained by kicking up loose heaps of hay, thistle stalks, or other rubbish, under which the mice take refuge. One specimen I have marked as found under a heap of thistle-stalks, in a round nest, the size of a tennis ball, made of thistle-down. Another was dug up, semi-torpid, in very cold weather, from about 6 inches below the surface of the ground." On an earlier occasion, Thomas (1898b, p. 3) recorded the same mice as *Oryzomys laucha* and remarked that in the city of La Plata, the species "inhabits the Museum park and the fields round the town and a specimen or two may generally be kicked out from under heaps of weeds or faggots left lying about the houses. Adult specimens are however by no means easy to obtain, and the great majority of those I saw and trapped were little more than half grown." Henry Durnford (*in* Thomas, 1898a, p. 211) noted that the *laucha* he collected in Chubut "makes a nest in a thick bush about a foot above the ground. The nest is made of grass torn into fine fragments." This information fits, rather, the scansorial *Eligmodontia* taken by Durnford at the same time.

A female *Calomys laucha* in captivity was studied by the Argentine epidemiologist Dr. J. M. de la Barrera (1936, p. 474). Mated July 30, 1935, the mouse produced a litter of 5 young on the 13th of September! Mated again October 2, 1935, it produced 3 young on the 26th of the same month. The last birth indicates a gestation period of approximately 25 days. This is normal for a small cricetine. The first litter, however, could not have required a gestation period of 43 days, as indicated by the dates. It is practically certain that there were two matings in this period, with offspring, if any, of the first destroyed by one or both parents; de la Barrera speaks of the female as being voracious and cannibalistic.

Nothing is known of the habits and circumstances of the importation of the Curaçao and Aruba *lauchas* described as *Baiomys hummelincki* by Husson in 1960. The type was collected in 1947. Other specimens examined by Husson date from 1930 (Aruba, P. Wagenaar Hummelinck, collector) to 1959 (Curaçao, J. H. Stock, collector). Presence of the species in the Netherlands West Indies was first reported in 1940 by Hummelinck (1940, p. 69) under the name *Hesperomys* sp.

The following account of the Venezuelan import colony is quoted from Butterworth (1960, p. 517):

"During the summer of 1958, Arnold Menke, Stephen Bromley and I made collections of animals in northeastern Venezuela for the Los Angeles County Museum. The facilities of the United Geophysical Corporation were made available to us, and part of our collecting was conducted from a temporary headquarters camp located 42 km. southeast of Maturin in the State of Monagas. Thirteen specimens of *Calomys laucha* were collected in the immediate area of the camp. . . . The present extension of the known range is possibly due to artificial introduction and establishment in the northern part of Venezuela. Units of the United Geophysical Company are also located in Bolivia, and equipment is frequently shipped back and forth between camps. It is possible that these mice were transported in equipment and subsequently became established in Venezuela.

"These short-tailed mice were timid creatures and seldom tried to escape when uncovered. All were collected by hand and, although they bite if molested, only one of them made an attempt to bite and escape. Four animals were found hiding under trash or boards in the camp area. Six had taken up residence in hollow logs and were found as far as 1000 feet from the camp in an adjacent marshy meadow.

"Of the thirteen specimens collected, nine were adults and four were juveniles. Five adult males had scrotal testes averaging 10 x 5 x 4 mm. All four adult females were pregnant. Three contained four embryos or fetuses ranging from 4 to 20 mm. (crown-rump); one female contained three fetuses measuring 12 mm.

"A nest containing three recently born young was uncovered under a board in the camp area. The nest was a shallow depression in the ground, lined with fine grasses. The mother stood over the young which lay on their backs while nursing. The hairless young measured approximately 36 mm. (total length) and had tightly closed eyes and ears. The mother later deserted the nest and the young were preserved in formalin."

Calomys laucha laucha Olfers

Rat septième ou rat laucha Azara, 1801, Quadrupèdes du Paraguay, **2**: 102.

Laucha Azara, 1802, Apuntamientos par la historia natural de los quadrúpedos del Paraguay y Río de La Plata, **2**: 96. Azara, 1809, Voyage Amérique Merid., **1**: 333.

[Mus?] laucha Illiger, 1815, Abh. Akad. Wiss. Berlin, **1804–1811**: 108—nomen nudum.

M[us] laucha Olfers, 1818, *in* Eschwege, Journal von Brasilien, Neue Bibliothek der Reisebeschreibungen zur Erweiterung der Erd- und Wölkerkunde, Weimar, **15**, (2): 209—PARAGUAY: name based on Azara's *laucha*. Brants, 1827, Het geschlacht des Muizen, p. 148—*laucha* Azara.

Mus laucha, Desmarest, 1819, Nouv. Dict. Hist. Nat., **29**: 65—*rat septième ou rat laucha* Azara. Desmarest, 1822, Mammalogie, **2**: 306.

H[esperomys] Laucha, Wagner, 1843, Schreber's Säugthiere, Suppl. **3**: 543—classification.

[Hesperomys] laucha, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 141—classification. Tate, 1932, Novit. Amer. Mus. Nat. Hist., no. 557, pp. 4, 5—taxonomic history.

Hesperomys laucha, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 182—ARGENTINA: *Corrientes* (Goya). Marelli, 1924, Elenco Sist. Fauna Prov. Buenos Aires, p. 671—ARGENTINA: *Buenos Aires; Tucumán*. Husson, 1960, Studies on the fauna of Curaçao and other Caribbean Islands, **10**, (43): 38—ARGENTINA: *Corrientes* (Goya); *Tucumán* (Concepción); comparisons.

Oryzomys laucha, Thomas, 1897, Ann. Mag. Nat. Hist., (6), **20**: 215 (in text)—PARAGUAY: (type locality); ARGENTINA: *Buenos Aires* (Bahía Blanca; Tala; La Plata); *Salta* (along Río Paraná to mouth). Thomas, 1898, Bol. Mus. Zool. Anat. Comp. Torino, **13**: 3—PARAGUAY: *Chaco* (Aguairenda); ARGENTINA: *Salta; Corrientes* (Goya); *Buenos Aires* (Tala; Buenos Aires; La Plata).

[Eligmodontia] laucha, Trouessart, 1904, Cat. Mamm., Suppl., p. 428—classification.

Eligmodontia laucha, Thomas, 1910, Ann. Mag. Nat. Hist., (8), **5**: 242—ARGENTINA: *Buenos Aires* (Los Inglesas).

Calomys laucha laucha, Hershkovitz, 1959, Jour. Mammal., **40**: 339—Azara's *laucha; bimaculatus* Waterhouse a synonym. Vaz Ferreira, 1960, Arch. Soc. Biol. Montevido, **24**: 67, fig. 1 (ears), figs. 2–5 (skull)—URUGUAY: *Artigas* (Salto; Tacuarembó); characters; habits.

Calomys laucha, Butterworth, 1960, Jour. Mammal., **41**: 517—VENEZUELA: *Monagas* (42 km. southeast of Maturín); habits.

Mus bimaculatus Waterhouse, 1837, Proc. Zool. Soc. London, **1837**: 18—URUGUAY: *Maldonado* (type locality, Maldonado). Waterhouse, 1839, Zool. Voy. "Beagle," pt. 2, pp. 42, 43, pl. 12 (animal), pl. 34, fig. 3 (skull, dentition)—description. Coues, 1874, Proc. Acad. Nat. Sci. Philadelphia, p. 177, footnote—part, type of *Hesperomys* Waterhouse by selection. Coues, 1877, Monogr. N. A. Rodentia, **1**: 44—type of *Hesperomys* Waterhouse.

Mus (Calomys) bimaculatus, Waterhouse, 1837, Proc. Zool. Soc. London, **1837**: 21.

Eligmodontia bimaculatus, Lesson, 1842, Nouv. Tabl. Reg. Anim., p. 133.

Hesperomys bimaculatus, Burmeister, 1861, Reise La Plata Staaten, **2**: 415—ARGENTINA: *Paraná; Tucumán;* may be Azara's *laucha*. Figueira, 1894, An. Mus. Nac. Montevideo, **2**: 17 (separate)—URUGUAY: throughout the country. Thomas, 1927, Ann. Mag. Nat. Hist., (9), **19**: 550—designation of lectotype and lectoparatype. Sanborn, 1929, Field Mus. Nat. Hist., Zool. Ser., **17**: 157—URUGUAY: *Minas* (Paso de las Averias, Río Cebollati; Polanco). Devincenzi, 1935, An. Mus. Hist. Nat. Montevideo, (2), **4**: 60—URUGUAY. Marelli, 1924, Elenco Sist. Fauna Prov. Buenos Aires, p. 671—ARGENTINA. Crespo, 1944, Rev. Argentina Zoogeogr., **4**: 138—ARGENTINA: *Buenos Aires* (San Miguel).

H[esperomys] bimaculatus, Burmeister, 1869, An. Mus. Publ. Buenos Aires, **1**: 457—*laucha* Azara. Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 141—classification; type of *Hesperomys*.

Hesperomys bimaculatus, Burmeister, 1879, Descr. Phys. Rep. Argentine, **3**: 224—ARGENTINA: eastern half of country; *Mus gracilipes* Waterhouse a young individual of *bimaculatus*.

H[esperomys (Calomys)] bimaculatus, Thomas, 1884, Proc. Zool. Soc. London, **1884**: 449, 454, pl. 44, fig. 14 (ear)—classification and measurements of type.

[Hesperomys] bimaculatus, Osgood, 1933, Field Mus. Nat. Hist., Zool. Ser., **20**: 14—URUGUAY: *Minas* (Polanco; Río Cebollati).

Calomys dubius bimaculatus, Cabrera, 1961, Rev. Mus. argentino Cienc. Nat. "Bernardino Rivadavia," **4**: 477—classification.

Mus gracilipes Waterhouse, 1837, Proc. Zool. Soc. London, **1837**: 19—ARGENTINA: *Buenos Aires* (type locality, Bahía Blanca). Waterhouse, 1839, Zool. Voy. "Beagle," pt. 2, pp. 42–45, pl. 11 (animal), pl. 34, fig. 4 (skull, dentition, hind foot)—description.

Mus (Calomys) gracilipes, Waterhouse, 1837, Proc. Zool. Soc. London, **1837**: 21—classification.

Eligmodontia gracilipes, Lesson, 1842, Nouv. Tabl. Regn. Anim., p. 133. Thomas, 1898, Proc. Zool. Soc. London, **1898**: 211. Allen, 1905, Exped. Patagonia, Princeton Univ., Mamm., p. 54—ARGENTINA.

[Hesperomys (Calomys) laucha] gracilipes, Trouessart, 1881, Bull. Soc. Etud. Scient., Angers, 1880, **10**, (1); 138—classification.

H[esperomys (Calomys)] gracilipes, Thomas, 1884, Proc. Zool. Soc. London, **1884**: 449—classification.

[Hesperomys] gracilipes, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 141—classification.

Mus pusillus Philippi, 1858, Arch. Naturg., (24), **1**: 79—CHILE: *Valparaiso* (type locality said to be the coastal region near Valparaiso). Philippi, 1900, Anal. Mus. Nac. Chile, Zool. Entr., **14a**: 19, pl. 5, fig. 2—type redescribed; regarded as conspecific with the *laucha* [=*Calomys laucha*]. Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 239—type redescribed; regarded as non-Chilean and probably an Argentine *Hesperomys* [=*Calomys*].

[Hesperomys (Akodon)] pusillus, Trouessart, 1881, Bull. Soc. Etud. Scient., Angers, 1880, **10**, (1): 142—classification.

[Akodon] pusillus, Trouessart, 1897, Cat. Mamm., p. 538—classification.

Akodon pusillus, Gyldenstolpe, 1932, Küngl. Sv. Vet. Akad. Handl., **11**, (3): 101—classification.

Eligmodontia laucha musculina, Thomas 1913, Ann. Mag. Nat. Hist., (8), **11**: 138—ARGENTINA: *Jujuy* (type locality, Maimará, 2230 meters altitude).

[*Hesperomys laucha*] *musculinus*, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 141—classification.

H[*esperomys*] *musculinus*, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 183—comparisons; 6 or 7 pairs of mammae.

Hesperomys musculinus, Thomas, 1920, Ann. Mag. Nat. Hist., (9), **6**: 116—ARGENTINA: *Catamarca* (La Puntilla, near Tinogasta). Thomas, 1926, op. cit., (9), **18**: 194—ARGENTINA: *Jujuy* (Santa Catalina).

Calomys laucha musculinus, Cabrera, 1961, Rev. Mus. argentino Cienc. Nat. "Bernardino Rivadavia," **4**: 479—classification; *cortensis* Thomas a synonym.

Hesperomys musculinus cortensis Thomas, 1920, Ann. Mag. Nat. Hist., (9), **5**: 190—ARGENTINA: *Jujuy* (type locality, Jujuy, 1258 meters altitude).

Hesperomys murillus Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 183—ARGENTINA: *Buenos Aires* (type locality, La Plata; Las Talas; Ensenada; Bahía Blanca).

Hesperomys murillus murillus, Yepes, 1935, Rev. Inst. Bacteriol., Buenos Aires, **7**: 227, pl. 6, fig. 2 (animal)—ARGENTINA: *Buenos Aires; Córdoba.*

Hesperomys murillus cordovensis Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 184—ARGENTINA: *Córdoba* (type locality, Yacanto, near Villa Dolores, 900 meters altitude). Thomas, 1919, op. cit., (9), **3**: 115—ARGENTINA: *Catamarca* (Chumbicha). Thomas, 1920, op. cit., (9), **6**: 116—ARGENTINA: *Catamarca* (La Puntilla, near Tinogasta). Thomas, 1921, op. cit., (9), **8**: 216—ARGENTINA: San Juán (Cañada Honda, 50 km. south of San Juán). Thomas, 1926, op. cit., (9), **17**: 322—BOLIVIA: *Tarija* (Tablada; Sama). Thomas, 1926, op. cit., (9), **17**: 604—ARGENTINA: *Tucumán* (Ñorco). Thomas, 1927, op. cit., (9), **20**: 204—ARGENTINA: *La Pampa* (Pichi Mahuida).

H[*esperomys*] *murillus cordobensis* [sic], Yepes, 1935, Rev. Inst. Bacteriol., **7**: 227—ARGENTINA: *Neuquén.*

Calomys laucha cordovensis, Cabrera, 1961, Rev. Mus. argentino Cienc. Nat. "Bernardino Rivadavia," **4**: 478—classification.

Hesperomys bimaculatus bonariensis Osgood, 1933, Field Mus. Nat. Hist., Zool. Ser., **20**: 14—ARGENTINA: *Buenos Aires* (type locality, Torrecita). Sanborn, 1947, Fieldiana, Zool., **32**: 242—type history.

Calomys dubius bonariensis, Cabrera, 1961, Rev. Mus. argentino Cienc. Nat. "Bernardino Rivadavia," **4**: 477—classification.

Baiomys hummelincki Husson, 1960, Studies on the fauna of Curaçao and other Caribbean Islands, **10**, (43): 34, fig. 7 (head, feet), pl. 6 (skull), pl. 7 (skull, molars)—NETHERLANDS ANTILLES: *Curaçao* (type locality, Klein Santa Martha; Plantation Jongbloed; Savonet Cave;

Sheribana); *Aruba* (Dakota Airport, Boca Morto; Barranca Corrá; Seroe Blanco). Husson, 1960, De zoogdieren van de Nederlandse Antillen, pp. 86, 157, fig. 21*a* (incisors), 22 (head, feet), pl. 26 (skull), pl. 30*b* (upper molars)—characters.

Hesperomys sp., Hummelinck, 1940, Studies on the fauna of Curaçao, Aruba, Bonaire and the Venezuelan Islands, The Hague, 1: 69—NETHERLANDS WEST INDIES: *Aruba* (Vadar Piet near Fontain); determination by M. A. C. Hinton and R. W. Hayman.

Calomys dubius dubius, Cabrera (part, not Fischer), 1961, Rev. Mus. argentino Cienc. Nat. "Bernardino Rivadavia," 4: 477—citation of "*Hesperomys bimaculatus bimaculatus* Yepes, Rev. Inst. Bacteriol., 7: 1935: 227" only.

Type.—None preserved; technical name based on Azara's published description of three specimens.

Type locality.—One of Azara's specimens was taken in a pile of maize stalks on a farm in the province of "Buenos Aires," and a second in the "pampas" about 25° S. Lat. Buenos Aires in Azara's time included present-day Uruguay and the Argentine provinces of Misiones, Corrientes and Entre Rios. Azara did no work in the modern province of Buenos Aires. The second locality, at the twenty-fifth parallel, may be construed as being in the neighborhood of Asunción, Paraguay, to which area the type locality is now restricted. Paraguay was selected by first reviser Olfers as type locality.

Distribution (fig. 37).—Paraguay, Uruguay and Argentina from Río Negro north into the Andean foothills of southern Bolivia. Altitudinal range from sea level to not over 2500 meters above. An established colony of imports 42 km. southeast of Maturín, Monagas, northeastern Venezuela, may have been transported from Bolivia, according to Butterworth (1960, p. 517). The precedence of the colonies in Curaçao and Aruba, Netherlands West Indies, has not been determined.

Characters.—Those of the species.

Variation.—Generally as given for the species. *Lauchas* from Uruguay and eastern Argentina are slightly darker throughout than those of the Argentine Andes. A series of 10 specimens from Guachalla and one specimen from Orloff, both localities in eastern Chaco, Paraguay, are nearest the Andean *lauchas* but average smaller and paler throughout with white under parts, lower third of sides of body, muzzle, arms and upper surface of hind feet. The Guachalla specimens, taken September 3–5, 1945, are in prime pelage; the Orloff individual, dated November 15, 1945, is in old worn pleage. There is complete agreement in external characters between the Guachalla specimens and the colored figure of the type of *Mus bimaculatus* Waterhouse (1839, pl. 12), taken in June.

Of 13 specimens from 42 kilometers southeast of Maturín, Monagas, Venezuela, which were collected and recorded by Butterworth (1960, p. 517), 4 are described as juvenals; the remaining 9, represented by skins and 6 skulls, are at hand. They include one juvenal and two subadults. Pelage of all is comparatively short and thin as in old summer pelage of their southern hemisphere relatives. Upper parts agree in color with the series from Guachalla, Chaco, Paraguay; under parts vary from white to grayish. The tail averages shorter, actually and relative to head and body length, than in any other series examined but in this respect they are also most like the Paraguayan *lauchas*.

Taxonomy.—First accurate characterization of mice of the restricted genus *Calomys* was presented by Felix Azara in the French edition (1801, p. 102) of his account of the mammals of Paraguay. The vernacular name "*laucha*" was applied to the three specimens described. In the later Spanish edition (1802, p. 96) only one *laucha* was described. There also appears in the Spanish edition a small mouse called "*blanco debaxo*" or white-bellied mouse. Tate (1932b, footnote, p. 11) thought the *blanco debaxo* was a *laucha* for which the technical name *Mus dubius* Fischer was available. Cabrera (1961, pp. 477–478) agreed and treated the white-bellied *bimaculatus* Waterhouse and the gray-bellied *bonariensis* Osgood, as subspecies of *Calomys dubius*.

Measurements given by Azara for the three *lauchas* of the French edition and those for the *laucha* and the *blanco debaxo* of the Spanish edition are as follows, in millimeters converted from Spanish inches.

		Edition	Total length	Tail	Hind foot with claw	Ear from crown
laucha	♂	French	110	46	15	7
laucha	♀	French	100	—	—	—
laucha	♀	French	81	—	—	—
laucha	—	Spanish	127	54	16	9
blanco debaxo	—	Spanish	135	42	18	13.5

External measurements of the *blanco debaxo* are not those of any known *Calomys*. The animal might be a *Thalpomys* but this possibility need not be discussed here.

Specimens from the type locality in the vicinity of Asunción are not available. Topotypes of *H. laucha laucha* may be nearer the small white-bellied specimens from Guachalla, Chaco, or they may be like the larger, darker Uruguayan and eastern Argentine *lauchas*. Whatever the affinities, too little is known of seasonal and geographic variation to prove subspecific distinction between any two populations of the species.

The figured skull accompanying the original description of the Uruguayan *Mus bimaculatus* Waterhouse (cited in the above synonymy) is inaccurate in several respects. It is shown with the interorbital constriction exaggerated and the nasals tapered behind to a point, instead of being square or broadly rounded. The mouse described and figured by Waterhouse (supra cit.) as *Mus gracilipes* is smaller than the type of *bimaculatus* but the difference in size lies well within the limits of individual variation. Measurements given by Gyldenstolpe (1932, p. 143) for "*Hesperomys gracilipes*" do not correspond to the type, as implied, or to any other member of the genus *Calomys*.

The body size of the type of *Hesperomys laucha musculinus* Thomas, from Maimará, Jujuy, equals that of small adults of the larger species *C. callosus* Rengger. However, the molar row length in *musculinus*, given as 3.6 mm., is diagnostic of *Calomys laucha*. Presumably because of the disparity in gross size between the types of *musculinus* and *laucha*, Thomas subsequently raised *musculinus* to specific rank and described *cortensis* as a subspecies of it. In this connection Thomas observed that the type series of *cortensis* included "a single old male skull—one of those overgrown examples which often render distinction of size so difficult—[that] measures no less than 26 mm. in greatest length; but this is obviously abnormal, the type being of about the usual adult size [24.5 mm.]." This statement adds weight to my opinion that the type of *musculinus*, also with skull length 26 mm., is an "overgrown" individual of *C. laucha*. Specimens at hand from the type region of *musculinus* and its erstwhile subspecies *cortensis* cannot be separated from other Argentine and Uruguayan *lauchas*.

Hesperomys murillus, described by Thomas in 1916, was recorded by the same authority in 1897 as *Oryzomys laucha* and again under this same name in 1898. Subsequent specific separation was based on the insignificant character of tail length, "which nearly or quite equals the head and body in length." *Hesperomys bimaculatus bonariensis* Osgood, like *murillus*, is nothing more than another name for the same small pampas *Calomys* already described from the same region as *laucha*, *bimaculatus* and *gracilipes*. No representative of

Hesperomys murillus cordovensis is at hand, but there is nothing in the original description or in the distributional pattern of related forms that suggests racial distinction of the Córdoba *laucha.* A specimen from Chumbicha, Catamarca, collected by Emilio Budin and identified by Thomas as *cordovensis,* is not separable from other Argentine lauchas.

The confusion attending the systematics of *Calomys* is compounded by use of such similar sounding trivial names as *murillus, muriculus, musculinus,* and *cortensis, cordovensis.*

Baiomys hummelincki Husson from the island of Curaçao, Netherlands West Indies, most nearly resembles new summer pelage representatives of typical *Calomys laucha laucha* but is more brightly colored ochraceous-buff and smaller throughout. The original description is based on a skin and skull (type) and a skull only from Curaçao, and four specimens from Aruba represented by two skins with skulls and two specimens in alcohol. External measurements given are minimal for *Calomys laucha* but were taken from the shrunken, preserved specimens. Cranial measurements are also small. The figure of the type skull and its greatest length, 18.6, are those of a juvenal. The largest skull, evidently of an adult, measures 19.3. The figures of the head and feet of one of the specimens in alcohol from Aruba are of a juvenal. Copies of these excellent drawings are used here (fig. 38) for illustrating the external characters of *Calomys laucha.* Husson's description of the Curaçao and Aruba specimens of *Calomys laucha* (=*Baiomys hummelincki*) and two skins and three skulls at hand of the same material agree best with the Venezuelan import colony. It has been suggested that the latter may have been transported from Bolivia but it is equally possible that it proceeded from Curaçao or Aruba. This still does not determine the native habitat or habitats of the original imports. In any event, the differences between the West Indian and Venezuelan populations are of the same order as differences between pocket populations in the southern hemisphere. Suppression of the winter pelage in the northern hemisphere *lauchas* is a niche variable. More collections are needed at regular intervals for measuring the rate of evolution of *Calomys laucha* in Venezuela and the Netherlands West Indies.

Measurements.—See Table 3 (p. 190).

Specimens examined.—67. PARAGUAY.—*Chaco:* Guachalla, 10 (CNHM); Orloff, 1 (CNHM). URUGUAY.—*Minas:* Paso de Averías, 2 (CNHM); Polanco, 1 (CNHM). ARGENTINA.—*Jujuy:*

Maimará, 2 (MACN). *Tucumán:* Concepción, 3 (CNHM). *Catamarca:* Chumbicha, 1 (CNHM). *Buenos Aires:* Torrecita, 13 including the type of *bonariensis* Osgood (CNHM); near Henderson, 4 (CNHM); Dorrego, 10 km. northwest, 7 (CNHM); Algarrobo, 2 (MACN). *Río Negro:* Chimpay, 7 (CNHM); Choele-Choel, 2 (MACN). VENEZUELA.—*Monagas:* Maturín, 9 (LACM). CURAÇAO.—Plantage Jongbloed, 1 (RNHL). ARUBA.—Shiribana, 1 (RNHL); Airport Dakota, Boca Morto, 1 (RNHL).

Calomys laucha tener Winge

Hesperomys tener Winge, 1888, E Mus. Lundii, **1**, no. 3: 15, pl. 2, fig. 3 (skull). Gyldenstolpe, 1932, Kungl. Sv. Vet. Akad. Handl., (3), **11**: 75—selection of lectotype.

[*Hesperomys*] *tener*, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 141—classification.

Eligmodontia tener, Shufeldt, 1926, Rev. Mus. Paulista, **14**: 503, 508, 563, 568, pl. 2, fig. 6 (skin)—BRAZIL: *São Paulo* (Piracicaba).

Type.—Female, Zoological Museum, Copenhagen, no. 252.

Type locality.—Rio das Velhas, Lagôa Santa, Minas Geraes, eastern Brazil.

Distribution (fig. 37).—Eastern Brazil; known from the states of Minas Geraes and São Paulo but probably occurs, also, in Goias and the southeastern coastal states of Brazil.

Characters.—The original description of *tener* is based on a comparison with the sympatric congener *Hesperomys callosus expulsus*. It remains to be shown that *tener* differs subspecifically from typical *laucha*.

Remarks.—Vieira (1953, p. 148) has recorded "*Hesperomys tener*" from São Paulo. Measurements given for two specimens are not those of any known species of *Calomys*.

Cabrera's (1961, p. 481) inclusion of "*Esperomys* [sic] *lepidus lepidus* Sanborn, Public. Mus. Javier Prado, Zool. num. 5, 1950: 3," in the synonymy of *Calomys tener* Winge is an obvious typographical error. Cabrera (op. cit., p. 480) cites the same reference correctly under *Calomys lepidus lepidus* Thomas.

Measurements.—Those of the lectotype and two cotypes are from the original description. External measurements taken from the dry skin: head and body, 95 ("stretched"), 82, 74; tail, 67 ("stretched"), 57, 61; hind foot, 16.5, 15, 16; ear, 13, 13.5, 12.5; greatest length of skull (of lectotype only), 19.7; zygomatic breadth, 12; upper molar row, 3.3.

Specimens examined.—None.

EXPLANATION OF FIGURE 39

Calomys lepidus: collecting localities and collectors.
Type localities in **boldface.**

Calomys lepidus lepidus (1–7)

PERU

1. Carhuamayo, Junín.—C. C. Sanborn at 14,500 feet.
2. **Junín, Junín.**—C. Jelski.
3. Tambo Polanco, San Miguel, Ayacucho.—C. Kalinowski.
4. San Jenaro, Santa Inéz, Huancavelica.—C. Kalinowski.
5. Lauramarca, Cusco (3996 meters).—O. Garlepp.
6. Lucre, Cusco.—O. Garlepp at 3500 meters.
6. Sucre, Cusco=Lucre (*q.v.*).
7. La Raya Pass, Cusco.—E. Heller at 14,010 feet.

Calomys lepidus ducillus (8–19)

PERU

8. **San Antón, Puno.**—P. O. Simons at 3800 meters.
9. Picotani, Puno.—C. C. Sanborn at 14,000 feet.
10. Posoconi, Puno.—C. C. Sanborn at 13,500 feet.
11. Santa Lucía, Puno.—M. R. Portugal.
12. Chucuito, Puno.—C. C. Sanborn.
13. Collacachi, Puno.—C. C. Sanborn.
14. Yunguyo, 6 miles south, Puno.—C. C. Sanborn at 13,000 feet.
15. Pairumani, Puno.—O. P. Pearson at 13,000 feet.
16. Huacullani, Puno.—C. C. Sanborn.
17. Sumbay, Arequipa.—C. C. Sanborn.
18. Salinas, Arequipa.—C. C. Sanborn and J. M. Schmidt at 13,500 feet.

CHILE

19. Ojos de San Pedro, Antofagasta.—C. Koford.

Calomys lepidus carillus (20–21)

BOLIVIA

20. La Cumbre, La Paz.—G. H. H. Tate at 15,200 feet.
21. **Choro, Cochabamba.**—P. O. Simons at 3500 meters; F. Steinbach at 3500 meters.

Calomys lepidus argurus (22)

ARGENTINA

22. **Abrapampa, Jujuy.**—E. Budin.

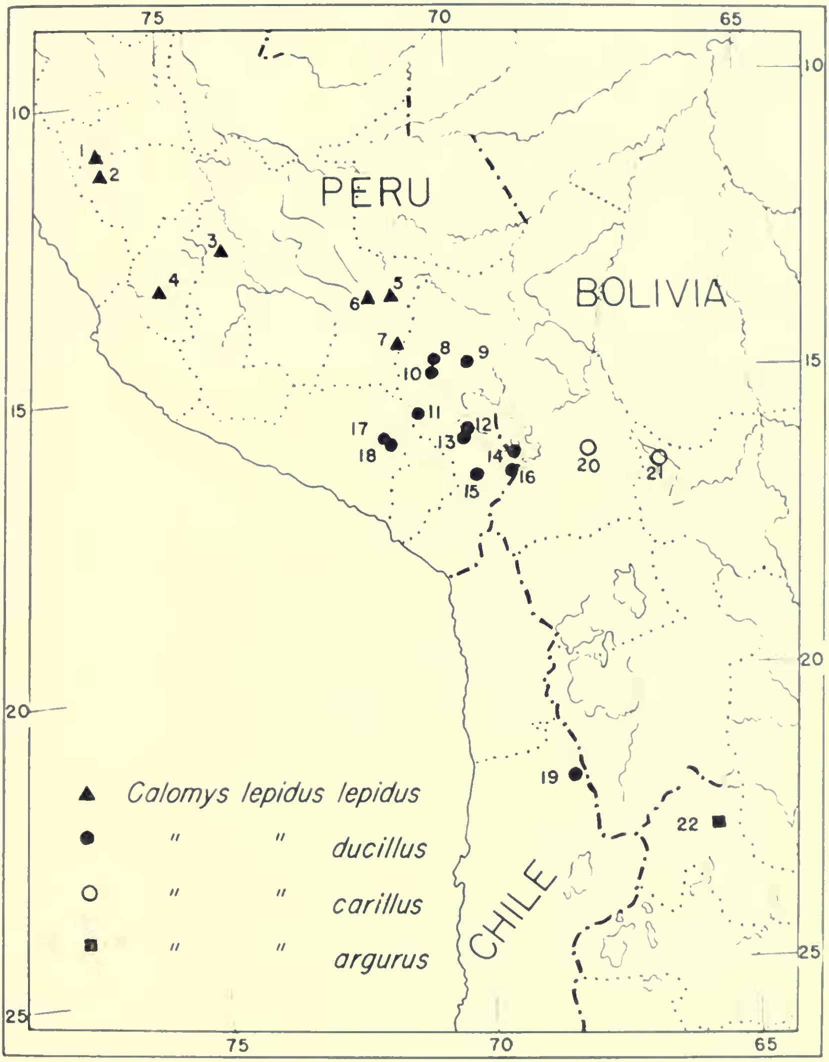

75
70
65
10
15
20
25
PERU
BOLIVIA
CHILE
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
▲ Calomys lepidus lepidus
● " " ducillus
○ " " carillus
■ " " argurus

FIG. 39.—Collecting localities of the subspecies of *Calomys lepidus*. See opposite page for explanation.

Calomys lepidus Thomas. (Synonymy under subspecies.)

Distribution (figs. 28, 39).—Temperate zone grasslands and scrublands of the southern half of Peru, western Bolivia, extreme northwestern Argentina and northeastern Chile; altitudinal range between 3000 and 5000 meters above sea level.

Characters.—Smallest of phyllotines in average size; pelage long, thick, smooth or crinkly; tail between one-third and two-thirds of length of head and body combined, whitish, buffy or gray above, slightly paler beneath, terminal portion sometimes darker than basal portion; fifth hind toe, less claw, not extending to tip of first phalanx of fourth toe; heel and proximal portion of sole hairy, the tarsal tubercle partially hidden; whitish postauricular patches present; upper parts of body buffy to tawny more or less suffused with gray anteriorly, lined or peppered with black posteriorly, the black tips of guard hairs prominent only in juvenals; under parts sharply defined gray or white with plumbeous basal portions of hairs showing through; lateral lines, when present, not well defined, often meeting posteriorly at base of tail; mammae 8 to 10 but usually not more than 6 detectable; supraorbital region of skull (figs. 29, 30, 40) parallel-sided or slightly concave mid-frontally, the edges square, never beaded; mid-frontal width less than greatest width of rostrum; posterior tip of lower incisor forming a ridge without capsular projection; dental characters (fig. 33) as for the genus.

Comparisons.—The small size and vole-like appearance are alone sufficient to distinguish *Calomys lepidus* from its three *Mus*-like congeners. Cranially, *C. lepidus* is nearest *sorellus*. The externally similar though much larger vole-like *Phyllotis sublimis* and *Galenomys garleppi* inhabit the same parts of the *altiplano* of southern Peru and western Bolivia. Juvenals of *Phyllotis sublimis* have been confused with adult *Calomys lepidus*, but differences between the two are obvious when size and shape of ears and hind feet, cranial characters, and size and structure of incisors and molars are taken into account.

Variation.—A bright buff, or tawny, color phase characterizes some series, and a dusky gray phase characterizes others. In the bright phase, head and shoulders are contrastingly grizzled in specimens from the more arid localities. In the dusky phase, upper parts and sides of body are fairly uniform in color except for the darker mid-dorsal line or band. Color of tail varies independently, but there are more dark tails among individuals of the dusky phase than in

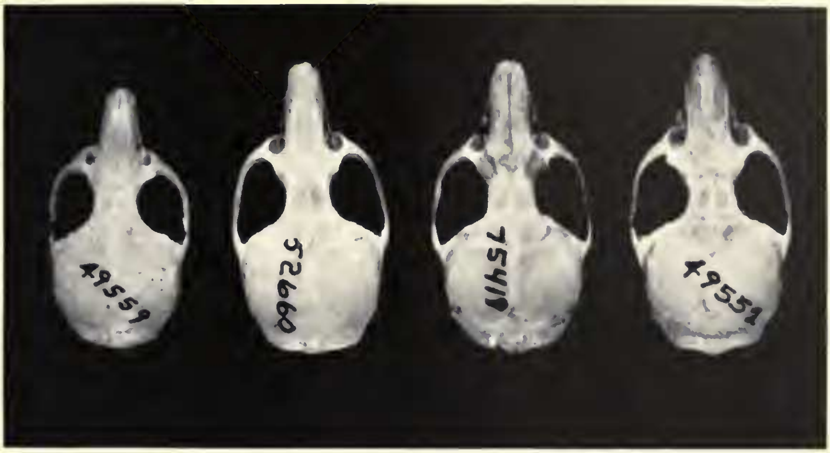


FIG. 40.—*Calomys lepidus.* Dorsal aspect of skulls showing variation in size (–× 2).

specimens of the bright phase. The color phases may represent two stages of seasonal pelage succession or each may be a constant in a given locality. The data are tabulated as follows:

Calomys lepidus lepidus (Peru)	No. of specimens	Date of capture	Phase
Carhuamayo, Junín	2	Feb. 21–23	bright
Tambo Polanco, Ayacucho	1	Nov. 27	dusky
San Jenaro, Huancavelica	1	Dec. 24	dusky
Calomys lepidus ducillus (Peru)			
Yunguyo, Puno	3	May 1–2	dusky
Posoconi, Puno	5	May 7–9	dusky
Santa Lucía, Puno	1	July 23	bright
Sumbay, Arequipa	1	Aug. 18	bright
Huacullani, Puno	3	Aug. 25–26	bright
Chucuito, Puno	1	Sept. 8	bright
Collacachi, Puno	8	Sept. 11–14	bright
Picotani, Puno	1	Sept. 15	bright
Salinas, Arequipa	5	Oct. 6–7	bright
Calomys lepidus carillus (Bolivia)			
Choro, Cochabamba	1	June 27	dusky
La Cumbre, La Paz	7	Feb. 12–15	dusky

Variation in tone of bright and dusky phases parallels the condition in *Phyllotis darwini* from the same localities. The bright Carhuamayo and dusky Ayacucho and Huancavelica specimens of *Calomys l. lepidus* are much more saturate than corresponding representatives of *C. l. ducillus*. The Bolivian *carillus* is represented by individuals of one color phase which are slightly darker than dusky specimens of *ducillus* and practically indistinguishable from dusky *lepidus*.

Most juvenals resemble small adults and growth continues throughout life.

Habits and habitat.—The following observations on *Calomys lepidus ducillus* are quoted from Pearson (1951, p. 141): "Only seven of these little mice were caught, most of them at night in grassy places or in stone walls such as those surrounding corrals in open country. *Hesperomys* was apparently more abundant than this catch indicates, for the owls at Pairumani (Puno, Lake Titicaca region) caught more *Hesperomys* than they did any other species. The nocturnal habits and grassland preferences of these mice make them natural owl prey, and it is possible that they are not attracted to trap baits (nuts were used for bait in most cases). *Phyllotis sublimis* was frequently trapped nearby.

"A female on August 29 had an open vagina and thick uterine horns, but no female earlier than this contained embryos and none was caught later. Two males in July had testes 5.5 and 7 mm. long.

"The only ticks encountered on any animal in the region were found on the ear of a *Hesperomys* from Pairumani."

The only other note on the habits of *Calomys lepidus* is a misleading one made by Thomas. In connection with the description of *C. lepidus argurus*, Thomas (1919d, p. 130) observed that it was the "dry-area representative of the forest *H. carillus*." The type and only specimen of *Calomys lepidus carillus* known to Thomas is from the grasslands of Choro, Cochabamba, in the Bolivian Andes.

Calomys lepidus lepidus Thomas

Hesperomys (Calomys) bimaculatus var. *lepidus* Thomas, 1884, Proc. Zool. Soc. London, **1884**: 454, pl. 42, fig. 2 (color), pl. 44, figs. 10, 11 (skull), fig. 12 (ear), fig. 13 (hind foot).

[*Hesperomys*] *lepidus*, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 141—classification.

E[*ligmodontia*] *lepida*, Thomas, 1900, Ann. Mag. Nat. Hist., (7), **6**: 298—comparison in text.

Hesperomys lepidus lepidus, Sanborn, 1950, Mus. Hist. Nat. "Javier Prado," (A), Zool., no. 5, p. 3—PERU: *Junín* (Carhuamayo).

Hesperomys carillus marcarum Thomas, 1917, Smithsonian Misc. Coll., **68**, no. 4, p. 1—PERU: *Cusco* (type locality, Lauramarca). Thomas, 1920, Proc. U. S. Nat. Mus., **58**: 231—PERU: *Cusco* (La Raya Pass; Sucre [=Lucre].

Calomys lepidus marcarum, Cabrera, 1961, Rev. Mus. argentino Cienc. Nat. "Bernardino Rivadavia," **4**: 480—classification.

Type.—Male, British Museum (Natural History) no. 85.4 1.43; collected by Constantin Jelski.

Type locality.—Junín, Junín, Peru.

Distribution (fig. 39).—Andes of central Peru in the Lago Junín and Ríos Apurimac–Urubamba drainage systems, departments of Junín, Huancavelica, Ayacucho, Apurimac and Cusco; altitudinal range, from approximately 3500 to 4500 meters above sea level.

Characters.—Upper parts tawny with or without a dark lining on posterior half.

Variation.—As described for the species (p. 160).

Remarks.—Specimens from Carhuamayo, Junín, are practically topotypes. One specimen from Huancavelica and another from Ayacucho agree with the published descriptions of *Calomys carillus marcarum* Thomas from Cusco. In view of the small difference of a clinal nature between *lepidus* of central Peru and *ducillus* of southern Peru the occurrence of a geographically intermediate race is extremely doubtful.

Measurements.—See Table 4 (p. 191).

Specimens examined.—4, all in collection of Chicago Natural History Museum. PERU.—*Junín:* Carhuamayo, 2. *Huancavelica:* San Jenaro, Santa Inéz, 1. *Ayacucho:* Tambo Polanco, San Miguel, 1.

Calomys lepidus ducillus Thomas

Eligmodontia ducilla Thomas, 1901, Ann. Mag. Nat. Hist., (7), **7**: 182.

[*Hesperomys*] *ducilla*, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 141—classification.

Hesperomys ducillus, Pearson, 1951, Bull. Mus. Comp. Zool., **106**: 141—PERU: *Puno* (Pairumani).

Hesperomys lepidus ducillus, Sanborn, 1950, Mus. Hist. Nat. "Javier Prado," (A), Zool., no. 5, p. 4—PERU: *Puno* (Posoconi; Hacienda Picotani; Chucuito; Hacienda Collacachi; Santa Lucía; Yunguyo); *Arequipa* (Salinas; Sumbay).

Hesperomys lepidus ducillus, Koford, 1954, Invest. Zool. Chilenas, **2**: 6, p. 95—CHILE: *Antofagasta* (Ojos de San Pedro).

Calomys lepidus ducillus, Cabrera, 1961, Rev. Mus. argentino Cienc. Nat. "Bernardino Rivadavia," **4**: 480—classification.

Type.—Female, British Museum (Natural History) no. 1.1.1.1; collected June 28, 1900, by Perry O. Simons.

Type locality.—San Antón, Lake Titicaca region, Puno, Peru; altitude, 3800 meters above sea level.

Distribution (fig. 39).—*Altiplano* of southern Peru, northeastern Chile, western Bolivia and probably northern Argentina; altitudinal range, 3500 to 4500 meters above sea level.

Characters.—Paler than typical *lepidus.*

Variation.—As described for the species (p. 160). The series from Salinas, another from Collacachi, and the only specimen from Huacullani exhibit a strongly contrasting grizzling on head and shoulders.

Remarks.—Specimens from Picotani and Posoconi are practically topotypical. The individual from the first locality is in the bright color phase, the series of five from the second locality is in the dusky pelage phase.

Measurements.—See Table 4 (p. 191).

Specimens examined.—28, all in collection of Chicago Natural History Museum. PERU.—*Arequipa:* Salinas, 5; Sumbay, 1. *Puno:* Huacullani, 3; Yunguyo, 6 miles south, 3; Santa Lucía, 1; Picotani, 1; Chucuito, 1; Posoconi, 3 miles west of Asillo, 5; Hacienda Collacachi, 8.

Calomys lepidus argurus Thomas

Hesperomys carillus argurus Thomas, 1919, Ann. Mag. Nat. Hist., (9), **4:** 130.

Type.—Female, British Museum (Natural History) no. 19.8.1.21; collected February 17, 1919, by Emilio Budin.

Type locality.—Abrapampa, Jujuy, Argentina; altitude, 3500 meters above sea level.

Distribution (fig. 39).—Known from type locality only.

Characters.—According to the original description, "essential characters apparently quite as in the true *H. carillus,* but colour throughout much paler."

Remarks.—The pale *argurus* may prove to be the northern Argentine representative of *Calomys lepidus ducillus.* Thomas ignored both *lepidus* and *ducillus* in his description of *argurus.*

Measurements.—See Table 4.

Specimens examined.—None.

Calomys lepidus carillus Thomas

Eligmodontia carilla Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9:** 133.

[*Hesperomys*] *carilla,* Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17:** 141—classification. Thomas, 1920, Proc. U. S. Nat. Mus., **58:** 231—comparison.

Hesperomys lepidus montanus Sanborn, (part), 1950, Mus. Hist. Nat. "Javier Prado," (A), Zool., no. 5, p. 4—BOLIVIA: *La Paz* (type locality, La Cumbre, 15,200 feet altitude); the type and one subadult only.

Type.—Male, British Museum (Natural History) no. 2.1.1.55; collected July 1, 1900, by Perry O. Simons.

Type locality.—Choro, Cochabamba, Bolivia; altitude 3500 meters above sea level.

Distribution (fig. 39).—Upper Río Madre de Dios drainage system in La Paz and Cochabamba Departments, Bolivia; altitudinal range, 3500 to 4800 meters above sea level.

Characters.—Slightly darker than dusky color phase representatives of *ducillus*.

Variation.—As for the species (p. 160).

Remarks.—The difference between dusky phase near topotypes of *Calomys lepidus ducillus* and Bolivian *carillus* is slight. However, the suspicion that the dark Bolivian specimens represent the bright color phase of *carillus* makes at least provisional recognition of the name advisable.

Hesperomys lepidus montanus Sanborn is based on a series of 4 subadults including the type, and 4 juvenals referable to *Phyllotis sublimis*. Two of the subadult *Calomys* are indistinguishable from a topotype of *carillus*, a specimen not available at the time of the description of *montanus*. The third subadult and, presumably, the type, are darker.

Measurements.—See Table 4 (p. 191).

Specimens examined.—4. BOLIVIA.—*Cochabamba:* Choro, 1 (CNHM). *La Paz:* La Cumbre, 3 (AMNH).

Calomys callosus Rengger. (Synonymy under subspecies.)

Distribution (figs. 28, 41).—Forest fringes and scrublands of southern Brazil, Paraguay, Bolivian Chaco; plains of northern Argentina, and eastern slopes of Andes from La Paz, Bolivia, into the Sierras Pampeanas in Argentina as far as Córdoba; altitudinal range from near sea level to approximately 200 meters above.

Characters.—Largest species of the genus; pelage long and moderately lax, or short and adpressed; tail from approximately 60 per cent to 90 per cent of combined head and body length, faintly to sharply bicolor; fifth hind toe, less claw, extending from base to middle of first phalanx of fourth toe; pale postauricular patches pres-

EXPLANATION OF FIGURE 41

Calomys callosus: collecting localities and collectors.

Type localities in **boldface.**

Calomys callosus callosus (1–29)

BOLIVIA (1–11)

1. Trinidad, Beni (236 meters).—R. H. Becker.
2. Pitiguaya, La Paz.—G. H. H. Tate at 5800 feet.
3. Astilleros, Yungas, La Paz.—P. O. Simons.
3. Río Solacamo, La Paz.—P. O. Simons at 1500 meters.
4. San Carlos, Ichilo, Santa Cruz.—F. Steinbach.
5. Buena Vista, Santa Cruz.—J. Steinbach at 500 meters.
6. San Antonio, Parapetí, Santa Cruz.—Marquis de Wavrin.
7. Tacuara, Chuquisaca.—J. Arauz.
8. Villa Montes, Tarija.—H. Krieg.
9. Tablada, Tarija.—E. Budin at 2000 meters.
10. Carapari, Tarija.—E. Budin at 1000 meters.
11. Yacuiba, "Tarija" (639 meters).—E. Budin at 600 meters; the town of Yacuiba is on the Argentine side of the boundary, in Salta Department.

BRAZIL (12–14)

12. Descalvados, Mato Grosso.—C. C. Sanborn.
13. Urucum de Corumbá, Mato Grosso.—C. C. Sanborn.
14. Rio Ivinheima, Mato Grosso.—F. Kühlhorn.

PARAGUAY (15–18)

15. Río Apa, Concepción.—Borelli.
16. Guachalla, Río Pilcomayo, Chaco.—P. Willem.
17. Pilcomayo (Río), 15 miles above mouth, Chaco.—P. Willem.
18. **Río Paraguay, opposite Río Bermejo, Villa del Pilar.**—J. R. Rengger.

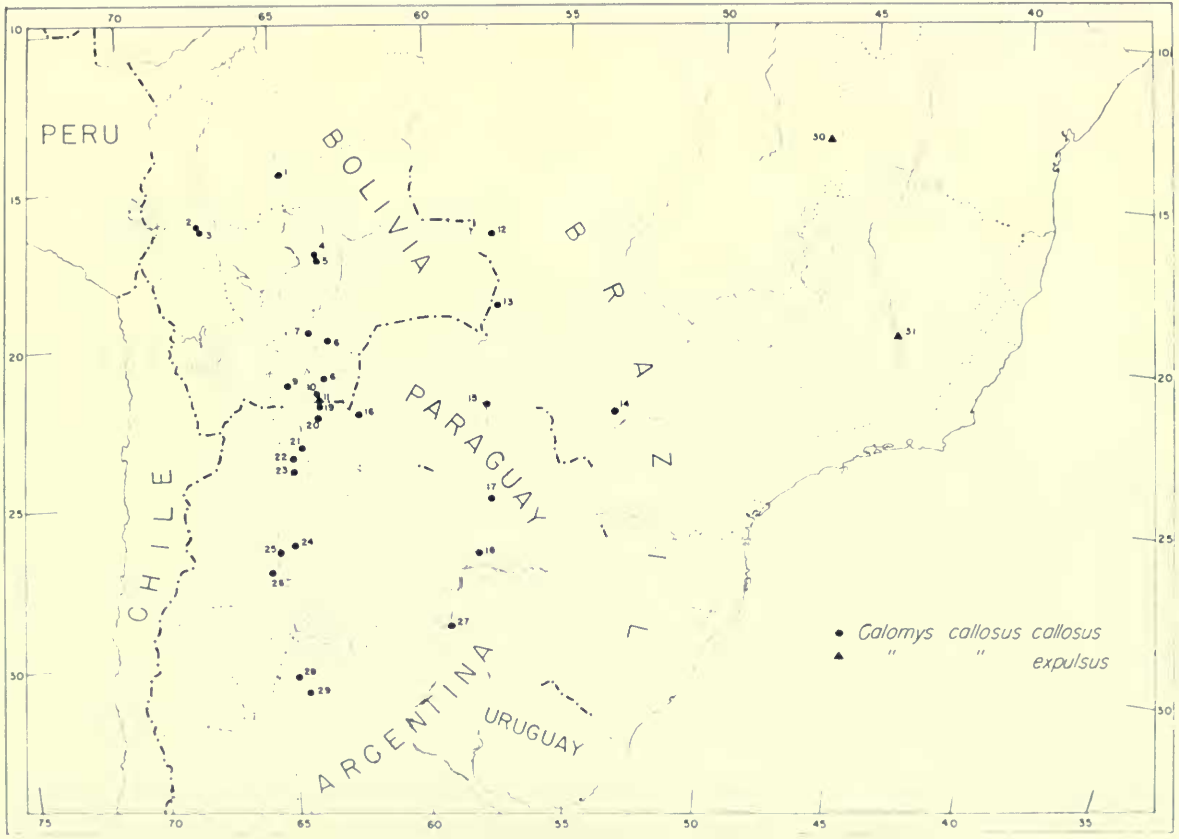
ARGENTINA (19–29)

19. Aguaray, Salta.—E. Budin at 700 meters.
20. Tartagal, Salta.—E. Budin at 600 meters.
21. Río Santa María, Salta.—J. Crespo.
22. Calilegua, Jujuy.—W. H. Osgood at 470 meters.
22. San Lorenzo, Jujuy.—Borelli.
23. Villa Carolina, Jujuy.—E. Budin at 500 meters.
24. Cerro del Campo, Burruyacu, Tucumán.—E. Budin at 800 meters.
25. Tafi Viejo, Tucumán.—E. Budin at 1000 meters.
26. Concepción, Tucumán.—F. Mogensen.
27. Goya, Corrientes.—R. Perrens.
28. Cruz del Eje, Córdoba (457 meters).—P. O. Simons at 600 meters.
29. Cosquín, Córdoba.—E. W. White.

Callomys callosus expulsus (30–31)

BRAZIL

30. Barro do Rio São Domingo, Goias.—J. Blaser.
31. **Lagôa Santa, Minas Gerais.**


PERU
BOLIVIA
BRAZIL
PARAGUAY
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● Calomys callosus callosus
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FIG. 41. Collecting localities of subspecies of *Calomys callosus*. See opposite page for explanation.

ent or absent; upper parts of body ochraceous to tawny with a fine or coarse mixture of black or dark brown; weakly defined ochraceous lateral band sometimes present; under parts gray with or without a thin buffy wash; mammae 8 to 14; borders of supraorbital region of skull (figs. 29, 30, 42, 54,*b*) divergent from anterior angle backward, strongly beaded and forming broad ledges in fully mature individuals; mid-frontal width always more than greatest width of rostrum; interparietal well developed; dental characters (figs. 43, 44, 56,*b*) as for the genus.

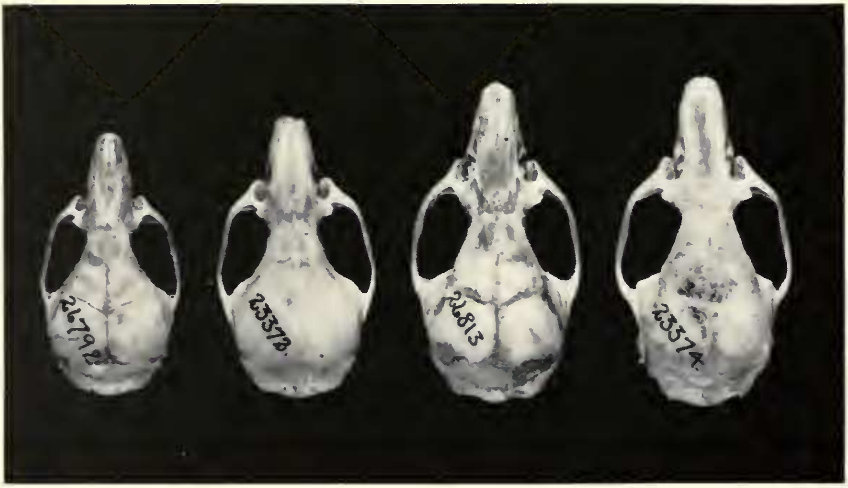

FIG. 42.—*Calomys callosus callosus.* Dorsal aspect of skulls showing variation in size (–×2).

Comparisons.—*Calomys callosus* is readily distinguished from all other members of the genus by larger size and specialized form of the supraorbital region. Large individuals of *C. callosus* resemble small ones of *Zygodontomys* (for comparison see p. 199 and figs. 34 and 44). *C. callosus* and *C. laucha* are sympatric throughout the greater part of their respective ranges. Both are *Mus*-like in appearance and, to a certain extent, in habits. Diagnostic characters given in the keys and descriptions are adequate for separating them.

Variation.—Individual and geographic variations in size lie within the same narrow limits. Color of adults in a given season is uniform throughout the range of the species. However, one specimen from Goias, Brazil, has dark under parts. Young individuals average darker than fully mature ones. Winter pelage is soft, long, and thick; summer pelage is short, thin and, in warmer localities, slightly hispid. Pattern of seasonal variation is local and, in Andean localities, may depend on altitude. Most marked condition of winter molt is found in specimens taken in June from Calilegua, Jujuy, and from localities in Tucumán. In a large series from Concepción, Tucumán, 3 specimens taken in May are in good pelage, 9 specimens taken in June are molting and 4 are in good pelage. In the same series, 2 specimens taken in December are in well-marked summer molt. Four specimens taken in February from Paraguay

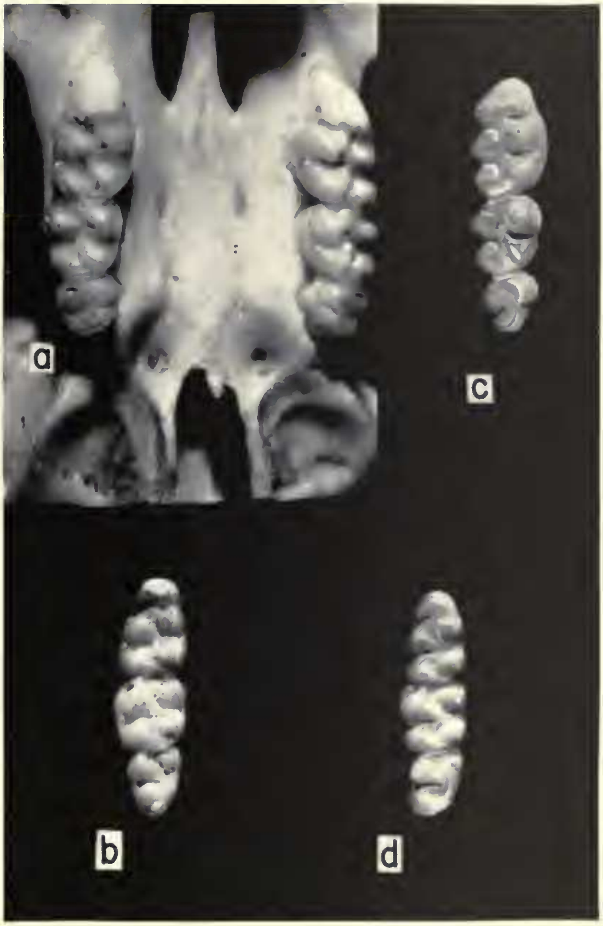

FIG. 43.—*Calomys callosus*. *a*, palate; *b*, lower molars of juvenal; *c*, *d*, worn upper and lower molars respectively, of adult.

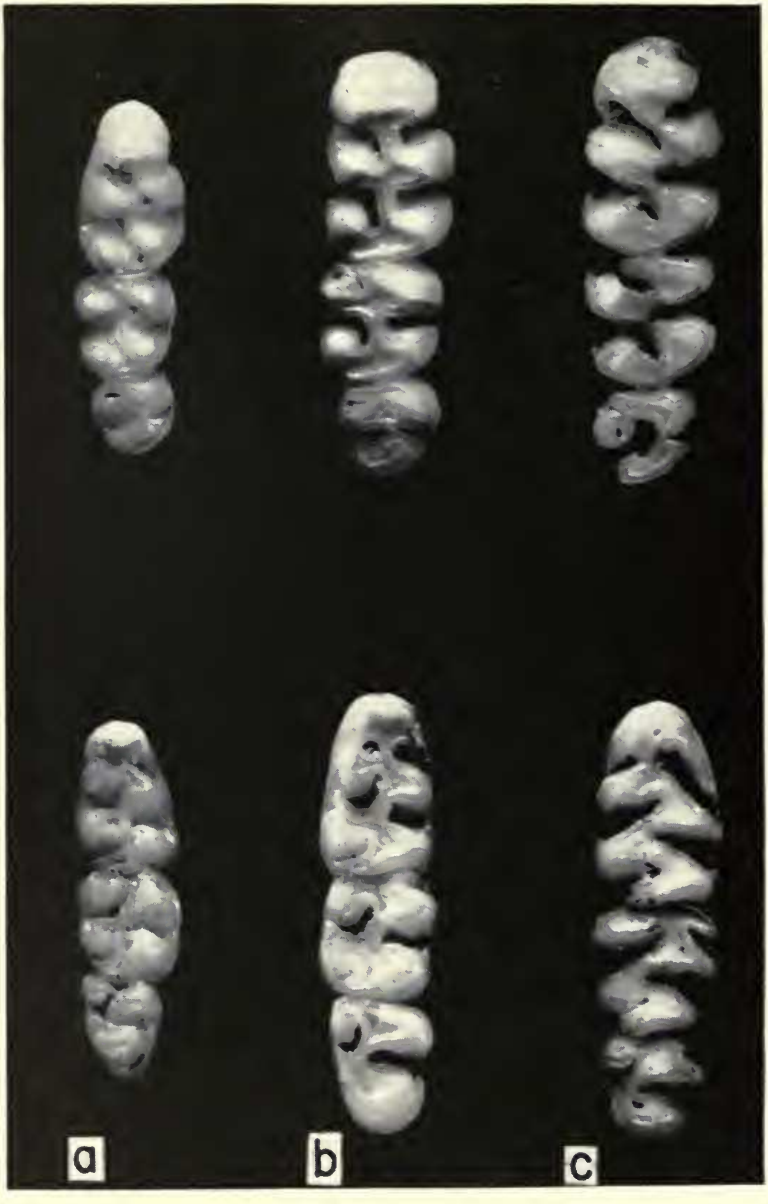

FIG. 44.—Upper and lower right molars of *a*, *Calomys callosus*; *b*, *Zygodontomys brevicauda*; *c*, *Phyllotis griseoflavus*.

have a short new summer pelage that averages darker than the longer winter pelage of other Paraguayan members of the species.

Habits and habitat.—*Calomys callosus* is the common mouse of gallery and scrub forests. It has invaded cultivated fields and houses, where it lives side by side with *Mus musculus.* In his description of *C. callosus,* Rengger stated that the mice dig tunnels several feet long by about two inches wide and nest there in pairs. Rengger also observed the species foraging in daylight for seeds and roots.

Rodents recorded by Kühlhorn (1952, p. 116; 1954, p. 72) as *Hesperomys musculinus* or *H. laucha musculinus* are certainly referable to the large species *Calomys callosus.* Their weight, given as 20–30 grams for subadults and 35–38 grams for fully developed individuals, corresponds to the weight of mice the size of *C. callosus* and averages more than twice the weight of mice the size of *C. laucha.* Kühlhorn's specimens were taken in gallery forest where *H. laucha* is unknown, and no specimens were found, after intensive trapping for several weeks, in open country, or in *campos,* where *H. laucha* might occur. Kühlhorn noted that the mice were most active at night but could still be observed in their runways between 6 and 7 o'clock in the morning. Although traps were always set, only one *Calomys* was taken at noon. The runways measured from 3 to 5 centimeters in width. Evidently, a mouse used only its own runway system. Once it was trapped out, no other mouse moved in. According to Kühlhorn, the species nests in holes in underbrush or rotting tree stumps. The above observations were made during the dry season in April and May, 1938. No nestlings, embryos or lactating females were taken at that time. Stomach contents revealed mainly vegetable matter with a small quantity of insects. Unfortunately, mice collected by Kühlhorn on Krieg's South American expedition were lost during the war.

Calomys callosus callosus Rengger

Mus callosus Rengger, 1830, Natürg. Säug. von Paraguay, Basle, p. 231. Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 182—species unidentifiable.

Oryzomys callosus, Thomas, 1898, Boll. Mus. Zool. Anat. Comp., Torino, **13**, no. 315, p. 3—PARAGUAY: *Concepción* (Río Apa, Concepción); *Chaco* (Río Pilcomayo); ARGENTINA: *Jujuy* (San Lorenzo); *Corrientes* (Goya).

Eligmodontia callosa, Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9**: 241—ARGENTINA: *Córdoba* (Cruz del Eje).

Hesperomys callosus, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 141—classification.

H[esperomys] callosus callosus, Yepes, 1935, Rev. Inst. Bacteriol., Buenos Aires, **7**: 227—ARGENTINA: all northern and central provinces.

Oryzomys (?) *venustus* Thomas, 1894, Ann. Mag. Nat. Hist., (6), **14**: 359—ARGENTINA: *Córdoba* (type locality, Cosquín).

[Hesperomys] venustus, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 141—classification.

Hesperomys venustus, Thomas, 1919, Ann. Mag. Nat. Hist., (9), **4**: 154—ARGENTINA: *Salta* (Tartagal). Thomas, 1920, op. cit., (9), **5**: 190—ARGENTINA: *Jujuy* (Villa Carolina). Thomas, 1925, op. cit., (9), **15**: 578—BOLIVIA: *Tarija* (Yacuiba; Carapari). Thomas, 1926, op. cit., (9), **17**: 604—ARGENTINA: *Tucumán* (Cerro del Campo, Burruyacu).

Calomys venustus venustus, Cabrera, 1961, Rev. Mus. argentino Cienc. Nat. "Bernardino Rivadavia," **4**: 481—*fecundus* Thomas, a synonym.

Eligmodontia callosa boliviae Thomas, 1901, Ann. Mag. Nat Hist., (7), **8**: 253—BOLIVIA: *La Paz* (type locality, Río Solocame, 1200 meters above sea level; Yungas; Astilleros).

[Hesperomys callosus] boliviae, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 141—classification.

Hesperomys callosus boliviae, Osgood, 1916, Field Mus. Nat. Hist., Zool. Ser., **10**: 207—BOLIVIA: *Beni* (Trinidad). Sanborn, 1950, Mus. Hist. Nat. "Javier Prado," (A), Zool., no. 5, p. 3—BOLIVIA: *La Paz* (Pitiguaya).

Hesperomys venustus callidus Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 182—ARGENTINA: *Corrientes* (type locality, Goya, altitude, 600 feet).

Hesperomys muriculus Thomas, 1921, Ann. Mag. Nat. Hist., (9), **8**: 623—BOLIVIA: *Santa Cruz* (type locality, San Antonio, Parapetí, about 250 km. south of Santa Cruz de la Sierra).

Hesperomys fecundus Thomas, 1926, Ann. Mag. Nat. Hist., (9), **17**: 321—BOLIVIA: *Tarija* (type locality, Tablada, altitude, 2000 meters).

Hesperomys musculinus, Kühlhorn (not Thomas), 1952, Zeitschr. Säugetierk., **18**: 116—habits.

Hesperomys laucha musculinus, Kühlhorn (not Thomas), 1954, Säugetierk. Mitt., **2**: 72—BRAZIL: *Mato Grosso* (Alto Paraná; Rio Ivinheima).

[?] *Necromys conifer* Ameghino, 1889, Act. Acad. Nac. Cienc. Córdoba, **6**: 120, pl. 4, figs. 17, 18 (dentition)—ARGENTINA: *Buenos Aires* (type locality, Buenos Aires [Pleistocene]).

Type.—Not known to be in existence. The bulk of Rengger's Paraguayan collection was lost before it could be sent to Europe. It is possible, however, that a few specimens reached the natural history museum of Aarau, Switzerland.

Type locality.—"Taken on the banks of the Río Paraguay at about 27 degrees latitude," i.e., opposite mouth of Río Bermejo, Department of Villa del Pilar, Paraguay.

Distribution (fig. 41).—Mato Grosso, Brazil, Paraguay, Bolivian Chaco, plains of northern Argentina and eastern slopes of Andes from La Paz, Bolivia, into the Sierras Pampeanas of Argentina as far south as Córdoba; altitudinal range to 2000 meters.

Characters.—Those of the species except that the under parts are not dark gray.

Taxonomy.—The original description of *Mus callosus* Rengger, published in 1830, is unmistakably that of the larger of the two known species of Paraguayan *Calomys*. There is absolutely no basis for the conjecture advanced by Thomas (1916b, p. 182) that *callosus* is the same as *Mus musculus*. Rengger compared *callosus with*, not *to*, as implied by Thomas, the Old World house mouse because the two animals are superficially similar and frequently occupy the same habitat. On pages 228–229 of his work Rengger makes clear the distinction between the "vier einheimische [cricetine] and zwei ausländische [murine] Nager" he found in Paraguay. Regarding measurements, those of *callosus* are practically the same as those of a number of specimens recorded or described by Thomas as members of the large species of *Hesperomys* (=*Calomys*). The name *callidus* proposed by Thomas for mice identified by authors as *callosus* Rengger is a gratuitous synonym.

The characterization of *Eligmodontia callosa boliviae* Thomas does not indicate substantial difference from Paraguayan *callosus*. Measurements of the types of the two forms are not significantly different, and specimens at hand from various localities in the Amazonian drainage of Bolivia are not separable from the Paraguayan form. The name *fecundus* is based on southern Bolivian individuals with nothing more distinctive than possession of 14 mammae instead of the more frequent 10. In addition to the type, Thomas recorded under the name *Hesperomys venustus* many specimens from various localities in northern Argentina and southern Bolivia. Abundant material at hand from the same regions shows nothing by which *venustus* can be separated from so-called *fecundus* or either of them from representatives of true *callosus*. Another named form of southern Bolivian *callosus* is *muriculus* Thomas. This is said to be "readily recognizable by its comparatively dark colour." Measurements and coloration of the type indicate a young individual. An adult from Tacuara, Chuquisaca, just northwest of San Antonio de Parapetí, type locality of *muriculus*, is indistinguishable from comparable specimens of *callosus*.

Measurements.—See Table 5 (p. 192).

Specimens examined.—113. BRAZIL. *Mato Grosso:* Descalvados, 7 (CNHM); Urucum de Corumbá, 9 (CNHM). BOLIVIA.

—*Beni:* Trinidad, 1 (CNHM). *Santa Cruz:* Buena Vista, 4 (MACN, 1; CNHM, 3); San Carlos, Ichilo, 2 (MACN, 1; CNHM, 1); Tacuara, 1 (CNHM). *Tarija:* Villa Montes, 2 (CNHM). PARAGUAY.—*Chaco:* Guachalla, Río Pilcomayo, 6 (CNHM); Río Pilcomayo, 15 miles above mouth at Río Paraguay, 5 (CNHM). ARGENTINA.—*Salta:* Aguaray, 3 (MACN); Río Santa María, 2 (MACN). *Jujuy:* Calilegua, 11 (CNHM). *Tucumán:* Burruyacu, 3 (CNHM); Tafi Viejo, 2 (MACN); Concepción, 55 (MACN, 3; CNHM, 52).

Calomys callosus expulsus Lund

Mus expulsus Lund, 1839, Ann. Sci. Nat., Paris, **11**: 233—BRAZIL: *Minas Gerais* (Rio das Velhas); name only. Lund, 1841, Afh. K. Danske Vidensk. Selsk. Nat. Math., **8**: 134, 266, 280, 294—description and records. Schinz, 1845, Syn. Mamm., **2**: 194—diagnosis.

Hesperomys expulsus, Burmeister, 1854, Syst. Ueber. Thiere Brasil, **1**: 175—BRAZIL: *Minas Gerais* (Lagôa Santa). Giebel, 1855, Odontographie, p. 50, pl. 21, fig. 7*b* (dentition). Giebel, 1857, Abh. naturw. Ver. Sächsen u. Thüringen, Halle, **1**: 191 seq., p. 5, fig. 8 (skull)—osteology. Winge, 1888, E Mus. Lundii, **1**, no. 3: 16 (description), pl. 1, fig. 1 (head), fig. 2 (hind foot), pl. 2, fig. 4 (skull), 4*a* (molar)—BRAZIL: *Minas Gerais* (Lagôa Santa). Gyldenstolpe, 1932, K. Sv. Vet. Akad. Handl., (3), **11**: 75.

[*Hesperomys*] *expulsus*, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 141—classification.

[*Oryzomys*] *expulsus*, Trouessart, 1898, Cat. Mamm., p. 528—classification.

[*Zygodontomys*] *expulsus*, Trouessart, 1905, Cat. Mamm., Suppl., p. 423.

Type.—In Zoological Museum, Copenhagen.

Type locality.—Lagôa Santa, Minas Gerais, Brazil.

Distribution (fig. 41).—Eastern Brazil; known only from Minas Gerais and Goias but the range probably extends from the Ríos São Francisco and Paraná to the coast.

Characters.—Possibly darker throughout than typical *callosus*.

Remarks.—Cotypes of *Mus expulsus* Lund have been redescribed and figured by Giebel (supra cit.) and Winge (supra cit.). The extremely detailed and accurate evidence leaves no doubt of the specific identity of *expulsus* with *callosus*. Subspecific status of *expulsus* may be postulated, however, on biogeographic grounds. A specimen from São Domingo, Goias, the only one examined that can be referred to *expulsus*, differs from typical *callosus* by its extremely dark under parts.

Measurements.—See Table 6 (p. 193).

Specimens examined.—1. BRAZIL.—*Goias:* Barro do Rio São Domingo, 1 (CNHM).

Genus **Eligmodontia** F. Cuvier

Eligmodontia F. Cuvier, 1837, Ann. Sci. Nat., Paris, Zool., (2), **7**: 168. Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 140—included species: *typus* Cuvier, type [*elegans* Waterhouse a synonym], *hirtipes* Thomas, *moreni* Thomas, *morgani* J. A. Allen.

Elygmodortia Wiegmann, 1838, Arch. Naturg., **4**: 388—misprint.

Heligmodontia Agassiz, 1846, Nomencl. Zool. Mamm., Addenda, **5**, Index Univ., pp. 136, 175—emendation.

Elimodon Wagner, 1841, Arch. Naturg., **1**: 125—misspelling. Palmer, 1904, N. Amer. Fauna, no. 23, p. 256—"*Elimodon*," cited from Fitzinger, 1867.

Eligmodon Thomas, 1896, Ann. Mag. Nat. Hist., (6), **18**: 307—emendation.

Type species.—Eligmodontia typus Cuvier.

Included species.—Eligmodontia typus Cuvier.

Distribution

Figures 27, 45

From the Straits of Magellan northward through Magallanes Chile into Argentina as far as the Río Paraná on the east, and along the Andes on the west into northern Chile, and the Lakes Poopo and Titicaca drainage basins of western Bolivia and extreme southern Peru; altitudinal range, sea level in southern latitudes, to more than 4500 meters above in higher latitudes.

EXPLANATION OF FIGURE 45

Eligmodontia typus: collecting localities and collectors.

Type localities in **boldface**.

Eligmodontia typus puerulus (1–12; 36–38)

CHILE (1–3)

1. Churiguaya(?), Puna Zone, Tarapacá. Presumably in vicinity of Parinacota; G. Mann.
2. San Pedro, 20 miles east, Antofagasta.—C. C. Sanborn at 12,600 feet.
3. **San Pedro de Atacama, Antofagasta** (3223 meters). F. Philippi.

BOLIVIA (4–6)

4. Oruro, Oruro.—P. O. Simons at 3700 meters.
5. Challapata, Oruro.—P. O. Simons at 3750 meters.
6. Pampa Aullagas.—P. O. Simons at 3800 meters.

ARGENTINA (7–12)

7. Abrapampa, Jujuy.—E. Budin at 3500 meters.
8. Chorillos, Los Andes (=Salta).—E. Budin at 4500 meters.
9. Corral Quemado, Catamarca.—E. S. Riggs.
10. Chumbicha, Catamarca.—E. Budin at 600 meters.

11. Chilecito, La Rioja.—F. P. Moreno at 1200 meters.
12. Media Agua, San Juán.—L. E. Miller and H. S. Boyle at 2200 feet.

PERU (36-38)

36. Santa Rosa, Puno.—O. P. Pearson at 14,000 feet.
37. Moquegua.—O. P. Pearson.
38. Tacna.—O. P. Pearson.

Eligmodontia typus typus (13–35)

ARGENTINA (13–34)

0. **Corrientes**, Department.—Supposed type region, but genus may not occur here.
13. Delta del Paraná, Buenos Aires.
14. Bahía Blanca, Buenos Aires.—C. Darwin.
15. Peru Station, F.C.O., La Pampa.—F. H. F. Parkes.
16. Pichi Mahuida, La Pampa.—E. Budin at 650 meters.
17. Chos Malal, Neuquén.—E. Budin at 800 meters.
18. Agrio (Río), Neuquén.—J. Yepes.
19. Zapala, Neuquén.—E. Budin at 1062 meters.
19. Las Lajas, Río Agrio, Neuquén.—E. Budin.
20. Choele-Choel, Río Negro.—E. Budin.
21. Pilcaniyeu, Río Negro.—H. E. Box; E. Budin.
22. Huanu Luan, Río Negro.—J. C. Peters.
23. Río Chubut, Chubut.—C. Burmeister.
23. Rawson, Chubut.—E. Budin.
24. Pico Salamanca, Chubut (=Comodoro Rivadavia).—E. Budin at 100 meters.
25. Piedra Clavada, Río Deseado, Santa Cruz (=Comodoro Rivadavia).—E. Budin at 200 meters.
26. Swan Lake, Santa Cruz.—A. E. Colburn.
27. Upper Río Chico, Santa Cruz.—A. E. Colburn.
28. Arroyo Else, Santa Cruz.—Used incorrectly for "Basaltic Canyons" (*q.v.*).
28. Basaltic Canyons, Santa Cruz.—Not precisely located, said to be "50 miles southeast of Lake Buenos Aires," but the Cordón Basáltico is at the point shown on map; A. E. Colburn.
29. Río Chico, Santa Cruz.—C. Burmeister.
30. Santa Cruz, Santa Cruz.
31. Coy Inlet, Santa Cruz.—O. A. Peterson.
31. Río Coy, Santa Cruz.—O. A. Peterson.
32. Halliday Ranch, Santa Cruz.—O. A. Peterson.
33. Cape Fairweather (=Cabo Buen Tiempo), Santa Cruz.—O. A. Peterson.
34. Río Gallegos, Santa Cruz.—E. Budin at 50 meters; O. A. Peterson.

CHILE

35. Sarmiento (Lake), Ultima Esperanza.—C. C. Sanborn.

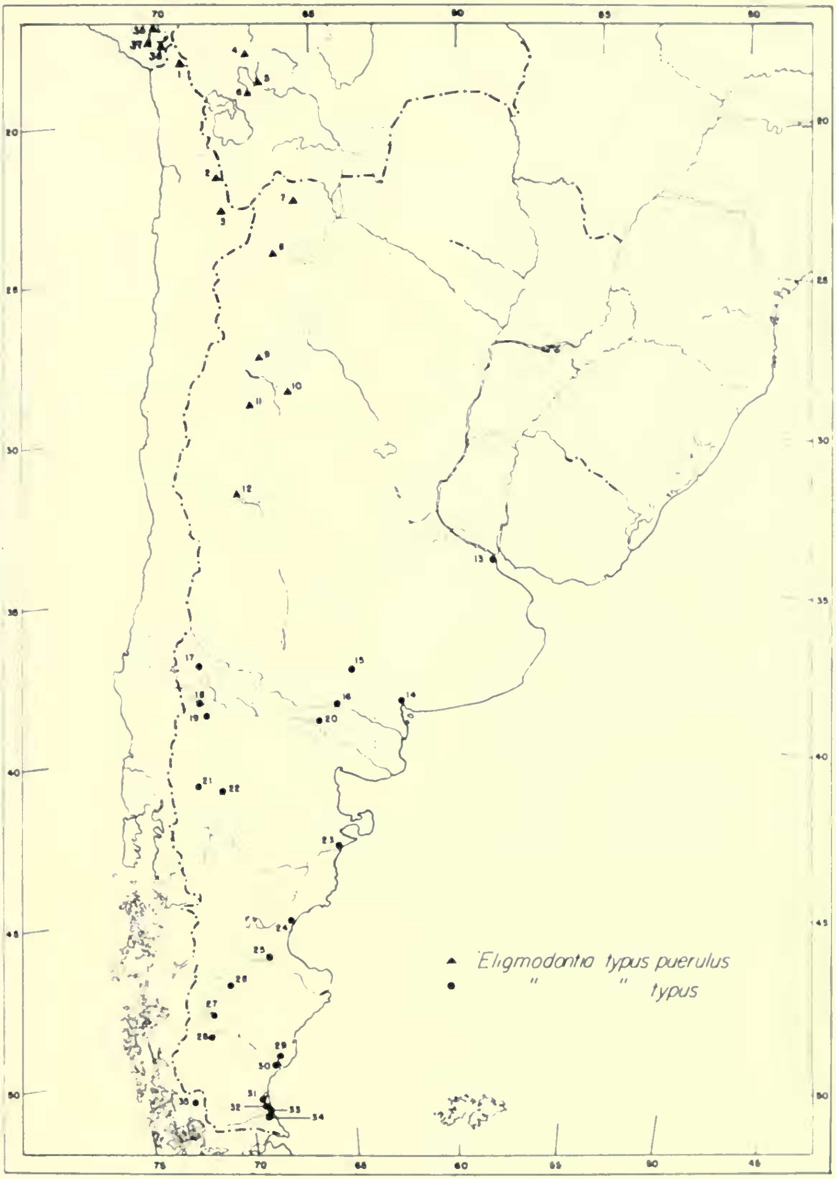
▲ Eligmodontia typus puerulus
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FIG. 45.— Collecting localities of subspecies of *Eligmodontia typus*. See opposite page for explanation.

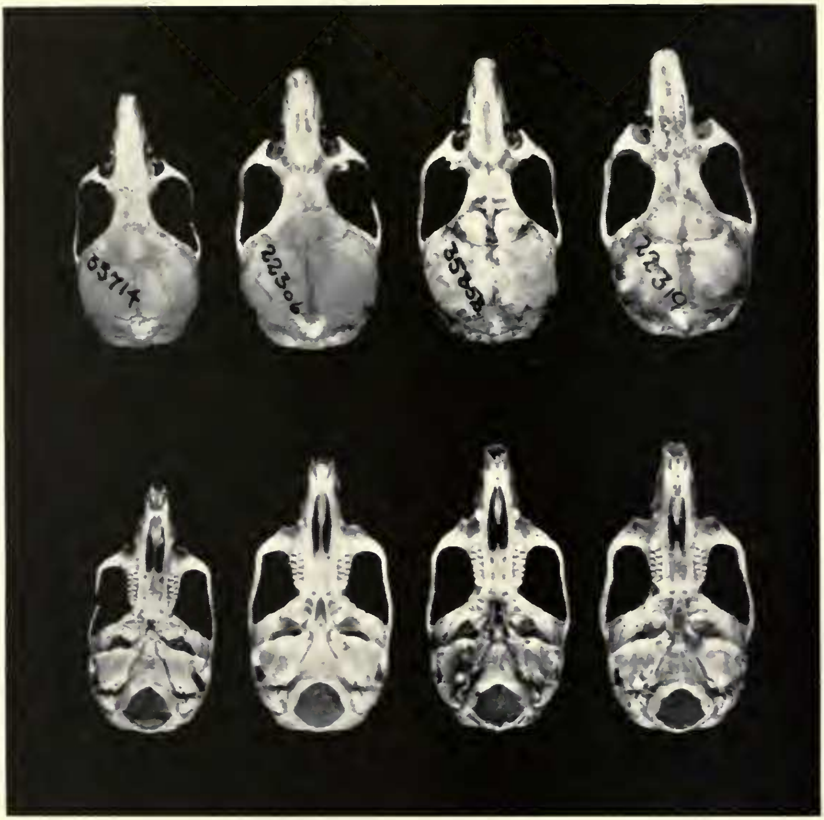

FIG. 46.—*Eligmodontia typus.* Dorsal and palatal aspects of skulls, showing variation in size (×1½).

Characters

External.—Small, gerbil-like in size, limb proportions, color and long, silky texture of pelage; upper parts buffy to tawny with a fine mixture of blackish giving a sandy effect in some series; under parts white, the hairs wholly white or plumbeous basally; tail from about 15 per cent shorter to about 15 per cent longer than combined head and body length, the pale under side from sharply to hardly defined from darker upper side; tip without conspicuous brush; hind legs elongated, metapodials broad, outer digits long, first hind toe without claw hardly extending to base of first phalanx of second, fifth toe without claw extending to base of second phalanx of fourth toe, claws well developed; soles (fig. 3) hairy except on tips of toes, first postdigital and tarsal tubercles; middle postdigital tubercles fused

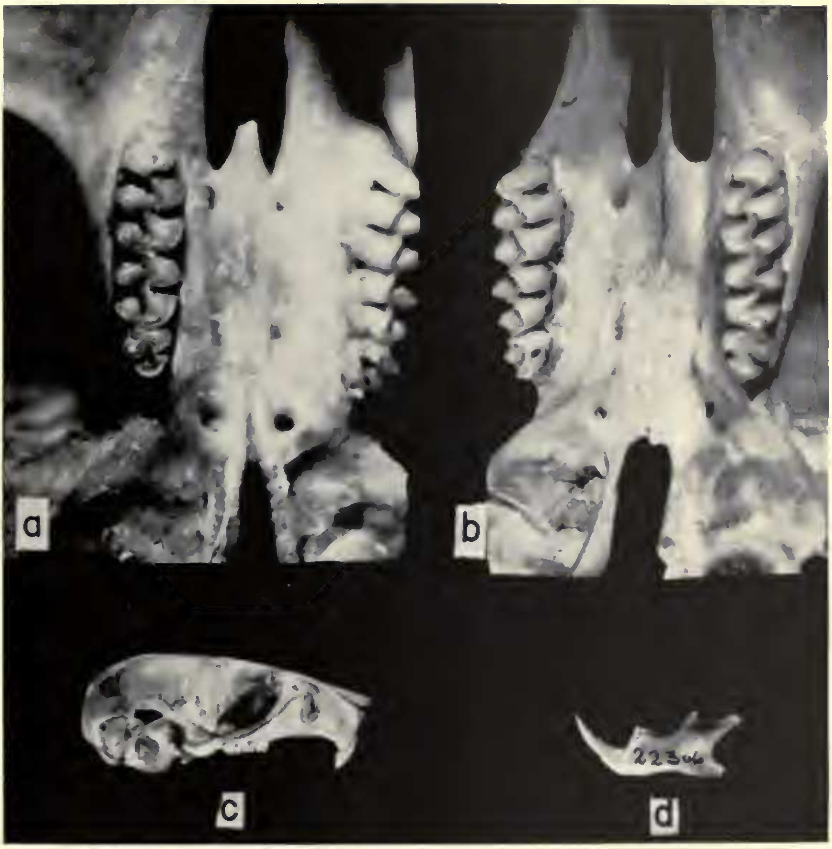

FIG. 47.—*Eligmodontia typus. a, b,* palate; *c,* skull; *d,* mandible.

to form a hairy cushion; fifth postdigital tubercle obsolete or absent; ears well developed but their length from notch always less than that of hind foot, small white postauricular patches present or absent; mammae, 2-2=8.

Cranial (figs. 46, 47).—Skull delicately built, dorsal contour flattened anteriorly, convex posteriorly, rostrum slender, its greatest width subequal to, usually less than, width of mid-frontal region; upper surface of skull with shallow median longitudinal depression; sinusoidal inflations of frontals reduced; sides of supraorbital region divergent, the edges square, never beaded or raised; outline of frontoparietal suture crescentic to nearly straight, never angular; braincase broad, smooth; interparietal well developed transversely, about five times wider than long; zygomata delicate, parallel-sided and little expanded; anterior border of zygomatic plate plane or slightly concave; bony palate produced well behind posterior plane of last molars; postero-lateral palatal depressions shallow, each marked by a conspicuous pit; a pair of anterior palatal pits present, one on each maxillary bone behind posterior end of incisive foramen; width of mesopterygoid fossa at anterior base of pterygoid processes usually less than greatest length of $m^{\underline{2}}$ and about one-half width of parapterygoid fossa measured at same plane; parapterygoid fossa comparatively shallow and broadly expanded laterally; bullae moderately inflated, length, less tubes, equal to or longer than alveolar length of molar row; mandibular ramus deeply excised posteriorly; condylar process about twice length of coronoid process and extending posteriorly to vertical plane of tip of angular process; capsular projection situated posteriad to angle of sigmoid notch.

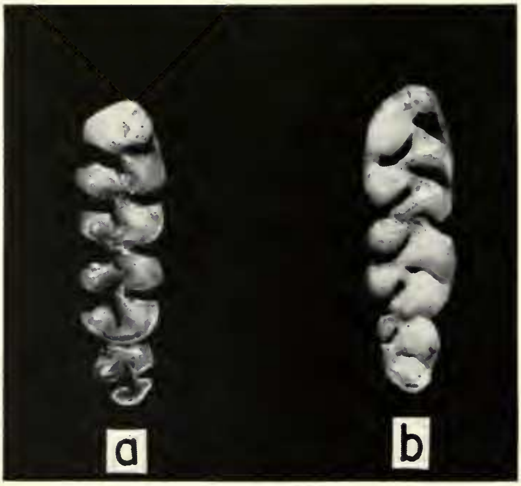

FIG. 48.—*Eligmodontia typus.* *a*, right upper molars; *b*, right lower molars.

Dental (figs. 48, 49).—Upper incisors opisthodont, ungrooved, molar rows parallel-sided or convergent posteriorly; upper and lower first molars four-rooted; $m_{\overline{3}}$ slightly more than one-half length of $m_{\overline{2}}$; cusps high, arranged in echelon, those of upper molars ovate, of $m_{\overline{1}-\overline{2}}$ tending to triangulation; mesostyle(id) absent; $m^{\underline{3}}$ without mesoloph and tending to lamination; $m_{\overline{3}}$ sigmoid in outline; upper and lower first molar with anterior fold well developed in unworn condition, weak or obsolete when worn; $m^{\underline{2}-\underline{3}}$ with anteroloph, the first primary fold well developed, never becoming an enamel island in m^2, rarely an island in worn m^3; second secondary fold indicated

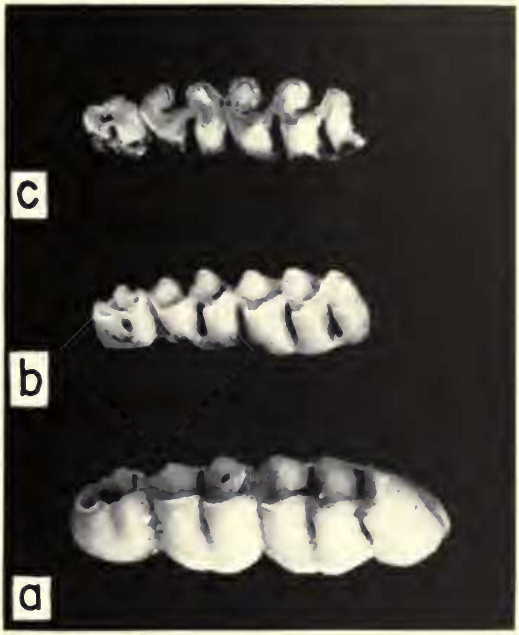

FIG. 49.—Molar planation. *a*, crested in *Zygodontomys; b*, bilevel crested in *Eligmodontia; c*, plane in *Phyllotis amicus*.

only in unworn m^{2-3}; first minor fold weakly developed or obsolete in m^2, obsolete in m^3; procingulum of m_{2-3} rudimentary or absent; minor fold present as a notch on enamel wall of m_2, as a minute enamel island in unworn m_3; second primary fold well developed and persistently open in m_{1-2}, obsolete in m_3.

Comparisons

The pale long silky pelage, long thin hind legs, and spade-shaped hind feet with a large hairy cushion on each sole, are salient external characters distinguishing *Eligmodontia* from all other living cricetines. Some of the Old World gerbils, notably *Gerbillus* (s. s.), are strikingly similar to *Eligmodontia* in size, bodily proportions, color and texture of pelage, and modification of the hind feet. In contrast, the closely related Piura desert mouse, *Phyllotis gerbillus*, is less similar superficially; its hind legs are not elongated, and the three middle postdigital tubercles are discrete and bare.

Cranially, *Eligmodontia* is nearest *Calomys* and most like *C. laucha*. The former is distinguished from the latter by such relative characters as longer rostrum, slightly more inflated braincase, frontals with little or no sinusoidal inflations, more pronounced dorsomedian longitudinal sulcus, less arched zygomata, and fronto-parietal sutures with less curvature.

The bilevel-crested, pre-terraced molars of *Eligmodontia* are annectant between the crested molars of *Calomys* and the terraced and plane molars of *Phyllotis* (fig. 49). Internal folds retained in some individuals of *Calomys* and mesostyle(id) usually present in *Zygodontomys*, are absent in *Eligmodontia*.

Remarks

Eligmodontia is the most highly specialized member of the *Calomys* section. Its ecological niche in the New World parallels that of *Gerbillus* in the Old World. Morphologically, *Eligmodontia* bridges the narrow gap between the *Calomys* and *Phyllotis* sections of phyllotine rodents.

Habits and Habitat

The capture of the type specimen of *Mus elegans* (=*Eligmodontia typus*) is described as follows by Charles Darwin (*in* Waterhouse, 1839, p. 42): " 'Whilst bivouacking one night on shore, amongst some sand hillocks, this mouse, with its tail singed, leapt out of a bush which was placed on the fire. Its hind legs appeared long in proportion to the front, and it did not appear to be very active in endeavouring to make its escape.' " Thomas (1898a, p. 210) has recorded Henry Durnford's observations on two specimens of *Eligmodontia* captured in Chubut, Argentina. The first is said to be " 'not uncommon among bushes, into which it climbs readily. Comes out in the evening to feed. I do not think this species makes holes in the ground.' " The second specimen bears this notation: "like the long-tailed rat [*Phyllotis griseoflavus*] this species is most numerous in the summer, though during the winter a few may be found. It does not enter the house like its large relative, but is extremely numerous in the thick scrub and brushwood in the neighborhood of the Colony, and universally distributed. It makes a small oval nest of fine grass and any soft material, which it places in the center of a thick bush. It never burrows in the ground, but is extremely numerous among the thorn bushes." During the course of their journey across the

Gobernación de Santa Cruz, Argentina, the Birabéns (1937, p. 160) found a nest of the mouse under a rock on the sea shore between San Julián and Bahía Laura. The nest was made of bits of sponge thrown up by the sea. Emilio Budin (*in* Thomas, 1919b, p. 202), who collected the same species in Pilcanieu, upper Río Negro, reports it as "common. Lives in holes at the foot of the bushes." The same collector referred to another specimen, the type of *jacunda* Thomas (1919d, p. 131), as having been "caught in sandy soil. Inhabits deserted burrows of Tuco-tucos [*Ctenomys*]." Budin took the type series of *marica* Thomas (1918, p. 483) among *pencas*, translated by Thomas as "prickly pears" but which are probably some species of maguey. Food in stomachs of *Eligmodontia* of northern Chile, examined by Mann (1945, p. 75), consisted largely of beetle larvae, with only a small fraction of vegetable matter.

Evidence from morphology, distributional records, and field observations indicates that *Eligmodontia* prefers a sandy or rocky terrain dominated by xerophytic plants. Because of the disproportionate length of fore and hind legs, the mouse walks clumsily on the ground and climbs slowly through brush. The long hind legs, however, permit the animal to accelerate its progress by bounding over level ground and leaping from rock to rock or among the branches and thick leaves of bushes. According to testimony, the mouse nests in shrubs, spiny bushes, and sometimes, whether for nesting or only for temporary asylum, in burrows not of its own making.

Eligmodontia typus Cuvier. (Synonymy under subspecies.)

Distribution and characters.—As for the genus.

Variation.—Dark and pale color phases are more sharply marked in *Eligmodontia* than in most other phyllotines. Nearly all *Eligmodontia* of the pampas and Patagonia of Argentina and Magallanes, Chile, are dark. The oldest name for them is *E. typus* Cuvier. Mice of the dry *salares* and *punas* of northern Argentina, northern Chile, and southwestern Bolivia average paler because of the greater number of pale phase individuals among them. The name *E. typus puerulus* Philippi is available for them.

Individual variation in size is striking. Under parts vary from wholly white to white with basal portions of hairs dark gray. As a rule, the more white on the under parts the greater the extension of white over lower half of sides of trunk, thighs, and arms. Pallid tails are usually correlated with pale bodies, but the difference in color between upper and lower surfaces of tail varies independently. Most variation in cranial characters is correlated with gross size differences. The rostrum, however, tends to be narrower and more tapered in some individuals and populations than in others. The shape of the anterior border of the zygomatic plate varies individually from straight to concave.

Eligmodontia typus typus Cuvier

Eligmodontia typus Cuvier, 1837, Ann. Sci. Nat., Paris, (2), **7**: 168, pl. 5 (animal, skull, molars, alimentary tract). Lesson, 1842, Nouv. Tabl. Règ. Anim., Mamm., p. 133—part, *elegans* Waterhouse in synonymy. D'Orbigny and Gervais, 1847, Voy. Amér. Mérid., **4**, Mamm., p. 24—ARGENTINA (type from Corrientes). Allen, 1905, Exped. Patagonia, Princeton Univ., **3**, Mamm., p. 51—*elegans* Waterhouse in synonymy. Marelli, 1924, Elenco Sist. Fauna Prov. Buenos Aires, p. 670—ARGENTINA: Delta del Paraná. Thomas, 1926, Ann. Mag. Nat. Hist., (9), **18**: 636—ARGENTINA: *Neuquén* (Chos Malal; Las Lajas; Zapala). Thomas, 1927, op. cit., (9), **19**: 652—ARGENTINA: *Neuquén* (Zapala). Thomas, 1927, op. cit., (9), **20**: 204—ARGENTINA: *Neuquén* (Pichi Mahuida). Yepes, 1939, Rev. Centro Doc. Estud. Cienc. Nat., **2**, (5): 9—ARGENTINA: *Neuquén* (Río Agrio).

E[ligmodontia] typus, Giebel, 1855, Odontographie, p. 51, pl. 23, fig. 10 (dentition). Thomas, 1918, Ann. Mag. Nat. Hist., (9), **2**: 483—"*elegans* is always assumed to be synonymous." Thomas, 1929, op. cit., (10), **4**: 39—ARGENTINA: *Corrientes* (type locality); *typus* for northern form, *elegans* for southern.

Mus elegans Waterhouse, 1837, Proc. Zool. Soc. London, **1837**: 19—ARGENTINA: *Buenos Aires* (type locality, Bahía Blanca). Waterhouse, 1839, Zool. Voy. "Beagle," pt. 2, p. 41, pl. 12 (animal), pl. 34, fig. 2 (skull, molars)—description; comparisons; identification with *typus* Cuvier.

Mus (*Cal[omys]*) *elegans*, Waterhouse, 1837, Proc. Zool. Soc. London, **1837**: 21.

Hesperomys elegans, H. Burmeister, 1879, Descr. Phys. Rép. Argentine, **3**: 220—ARGENTINA: *Chubut* (Río Chubut).

H[esperomys] elegans, C. Burmeister, 1891, Anal. Mus. Nac. Buenos Aires, **3**: 314—ARGENTINA: *Santa Cruz* (Río Chico).

H[esperomys Calomys] elegans, Thomas, 1884, Proc. Zool. Soc. London, **1884**: 449—classification.

E[ligmodon] elegans, Thomas, 1896, Ann. Mag. Nat. Hist., (6), **18**: 308—synonym of *E. typus*.

Eligmodontia elegans, Thomas, 1898, Proc. Zool. Soc. London, **1898**: 210—ARGENTINA: *Chubut;* habits. Thomas, 1929, Ann. Mag. Nat. Hist., (10), **4**: 39—ARGENTINA: *Chubut* (Pico Salamanca); *Santa Cruz* (Piedra Clavada; Río Gallegos); synonyms, *E. morgani* Allen, *pamparum* Thomas. Yepes, 1939, Rev. Centro Doc. Estud. Cienc. Nat., **2**: 5—ARGENTINA: *Neuquén* (Chos Malal). Gyldenstolpe, 1932, K. Sv. Vet. Akad. Handl., **11**: 70, 162, pl. 7, fig. 3 (skull), pl. 17, fig. 19 (molars)—ARGENTINA: *Río Negro* (Pichi Mahuida).

Eligmodontia morgani Allen, 1901, Bull. Amer. Mus. Nat. Hist., **14**: 409—ARGENTINA: (type locality, "Arroyo Else, Patagonia"). Allen, 1905, Exped. Patagonia, Princeton Univ., **3**, Mamm., p. 53, pl. 9, fig. 1 (skull), pl. 10, figs. 2, 3 (molars)—ARGENTINA: *Santa Cruz* (type locality, "Basaltic Cañons, 50 miles southeast of Lake Buenos Aires, Patagonia," not "Arroyo Else" on the labels and in the original description; Río Gallegos; Halliday Ranch; Coy Inlet; Cape Fairweather; upper Río Chico; Basalt Cañons; Swan Lake). Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 141—classification. Thomas, 1919, Ann. Mag. Nat. Hist., (9), **3**: 202—ARGENTINA: *Río Negro* (Pilcañeu). Birabén and Scott, 1936, Rev. Mus. La Plata, (n.s.), sec. oficial 1936, p. 160—ARGENTINA: *Santa Cruz* (coast). Cabrera, 1936, *in* Birabén and Scott, loc. cit.,—perhaps a subspecies of *E. typus.*

Eligmodontia elegans morgani, Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 199—ARGENTINA: *Santa Cruz* (Piedra Clavada; Río Coy; Río Gallegos); CHILE: *Magallanes* (Lake Sarmiento, Ultima Esperanza).

Eligmodontia morgani pamparum Thomas, 1913, Ann. Mag. Nat. Hist., (8), **12**: 572—ARGENTINA: La Pampa (type locality, Peru Station, F. C. O.).

Type.—Presumably in the Museum National d'Histoire Naturelle, Paris; collected by Alcide d'Orbigny.

Type locality.—"Buenos Aires," but according to d'Orbigny (supra cit.) "province de Corrientes," Argentina. The "Buenos Aires" locality, as given in the original description by Cuvier, was meant to encompass most of central and northern Argentina, including Corrientes. There is a question of whether or not the genus actually occurs in the modern department of Corrientes or anywhere north and east of the Río Paraná.

Distribution (map, fig. 45).—Southern Chile and Argentina, from the Straits of Magellan north through Magallanes, Chile and in Argentina into the provinces of La Pampa and Buenos Aires. Occurrence of *Eligmodontia* north and east of the Río Paraná has not been corroborated and its existence there is extremely doubtful.

Characters.—A sandy-colored mouse, sides slightly paler than upper parts, except for a narrow, not always well-defined, ochraceous lateral line; tail brown above, nearly as dark below, or sharply bicolor.

Taxonomy.—In his description of *elegans,* Waterhouse made it clear both in text and synonymy that his specimen and Cuvier's *typus* "are identical." The synonymy was pointed out again by Thomas, first in 1896, then in 1916, 1918, and finally in 1929. J. A. Allen, in 1905, also called attention to the priority of the name *typus* Cuvier, published March 1837, over that of *elegans* Waterhouse, dated November 21, 1837. Nevertheless, Allen added *morgani* and Thomas added *pamparum*, both names later shown by Thomas himself (supra cit., 1929), to be synonyms of the synonym *elegans*.

Measurements.—See Table 7 (p. 194).

Specimens examined.—19. ARGENTINA.—*Río Negro* (Pilcaniyeu, 1 (CNHM); Huanu Luan, 1 (CNHM); Choele-Choel, 3 (CNHM, 1; MACN, 2). *Neuquén:* Chos Malal, 3 (CNHM); Las Lajas, 1 (CNHM). *Chubut:* Rawson, 2 (MACN). *Santa Cruz:* Santa Cruz, 3 (CNHM); Piedra Clavada, 1 (CNHM); Río Gallegos, 1 (CNHM); Cabo Buen Tiempo (Cape Fairweather), 1 (CNHM); Río Coyle (Río Coy), 1 (CNHM). CHILE.—*Magallanes:* Lake Sarmiento, Ultima Esperanza, 1 (CNHM).

Eligmodontia typus puerulus Philippi

Hesperomys puerulus Philippi, 1896 [sic], Anal. Mus. Nac. Chile, Zool. Ent., 13a, p. 20, pl. 7, fig. 1 (animal).

Mus puerulus, Philippi, 1900, Anal. Mus. Nac. Chile, Zool. Ent., 14a, p. 60.

Eligmodontia puerulus, Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30:** 198, fig. 27 (skull)—CHILE: *Antofagasta* (San Pedro, 20 miles east); redescription of type.

E[ligmodontia] p[uerulus] puerulus, Mann, 1945, Biológica, Univ. Chile, fasc. 2, p. 78 (comparisons).

Eligmodontia puerulus puerulus, Pearson, 1957, Breviora, Mus. Comp. Zool., Harvard, no. 73: 2—PERU: *Moquegua; Puno; Tacna;* altitudes, 13,000–15,300 feet.

Eligmodon Moreni Thomas, 1896, Ann. Mag. Nat. Hist., (6), **18:** 307—ARGENTINA: *La Rioja* (type locality, Chilecito, 1200 meters altitude). Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17:** 141—classification.

Eligmodontia typus morenoi, Cabrera, 1961, Rev. Mus. argentino Cienc. Nat. "Bernardino Rivadavia," **4:** 482—classification.

Phyllotis hirtipes Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9:** 225—BOLIVIA: *Oruro* (type locality, Challapata, Lake Poopo, 3750 meters altitude; Oruro; Pampa Aullagas).

Eligmodontia hirtipes, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17:** 141—classification.

Eligmodontia puerulus hirtipes, Mann, 1945, Biológica, Univ. Chile, fasc. 2, p. 78—classification; comparisons. Pearson, 1951, Bull. Mus. Comp. Zool., **106:** 142—PERU: *Puno* (Santa Rosa).

Eligmodontia marica Thomas, 1918, Ann. Mag. Nat. Hist., (9), **2:** 483—ARGENTINA: *Catamarca* (type locality, Chumbicha, 600 meters altitude). Thomas, 1919, op. cit., (9), **3:** 115—ARGENTINA: *Catamarca* (desert area east of Chumbicha).

Eligmodontia hirtipes jacunda Thomas, 1919, Ann. Mag. Nat. Hist., (9), **4:** 131—ARGENTINA: *Jujuy* (type locality, Abrapampa, 3500 meters altitude).

Eligmodontia puerulus tarapacensis Mann, 1945, Biológica, Univ. Chile, fasc. 2, p. 75, fig. 25 (feet), figs. 26, 27 (alimentary tract), fig. 28 (zygomatic plate), pl. 28 (skin)—CHILE: *Tarapacá* (type locality, "Churiguaya" puna zone). Mann, 1950, Invest. Zool. Chilenas, **1**, (2): 5—CHILE: *Tarapacá.*

Type.—Skin, mounted, Museo Nacional de Chile; collected by Federico Philippi between 1884 and 1885.

Type locality.—San Pedro de Atacama, Antofagasta, Chile; altitude, 3223 meters above sea level.

Distribution (map, fig. 45).—Sierras Pampeanas and Andes of northern Argentina from the province of San Juan northward into the *puna* zones, lake, and *salar* basins of western Bolivia, northwestern Chile and extreme southern Peru; altitudinal range from approximately 500 to 4800 meters above sea level.

Characters.—Slightly paler throughout than *typus;* back less mixed with blackish, tail pale brown or grayish above, paler beneath, to nearly uniformly whitish.

Remarks.—The original publication of the name *Hesperomys puerulus* Philippi is dated 1896. However, the bibliographic section for 1894 of the Archiv für Naturgeschichte (1896, Jahrg. 62, **2**: 234) records the date of publication as 1890. Whatever the date, the name *puerulus* clearly has priority over *moreni*, described by Thomas in October 1896.

According to Osgood (supra cit.) the type of *puerulus*, in the Santiago de Chile Museum, is "not so brightly ochraceous as in Philippi's figure, and is more of a pale buff with a cinnamon-tipped effect. On the under side . . . the hairs are white to the roots on the throat, chest, inguinal region, and probably along middle line of abdomen. Laterally on the abdomen, the hairs have light grayish plumbeous bases. The soles of the hind feet seem to be hairy, but this is not well ascertained. Hind foot measures 21.5 [presumably with claw]. The tip of the tail is not quite perfect, but apparently it was slightly pencilled.

"The small size of the hind foot in the type is the only feature to cast any doubt upon its identity with the small series now at hand in which the foot measures 24, 25, 25, 25, and 26 mm. Other characters of the type, especially the pure white under parts and general proportions, seem to outweigh this, and with a series from the type locality showing these characters, the establishment of the name is amply justified."

The five specimens mentioned above by Osgood are from Río San Pedro, 3940 meters above sea level, and 20 miles east of San

Pedro, a station on the Antofagasta-Bolivian railroad. The locality is in the *puna* zone about 115 kilometers north of San Pedro de Atacama, where the type of *puerulus* was taken. The specimens, all in dark phase, are insignificantly paler, especially on the tail, than Argentina *typus*.

The northern Chilean form described as *Eligmodontia puerulus tarapacensis* by Mann is said to differ from Philippi's *puerulus* by paler color of dorsum and bicolor tail. The tail of the type of *puerulus* is shown in the original figure to be sharply bicolor, hence as in *tarapacensis*. Tails in the Río San Pedro series vary from sharply bicolor to faintly so. Color of back is the tenuous character that distinguishes pale from dark phase individuals.

Thomas described *moreni* as "most nearly allied to *E. elegans*, Waterh. (*E. typus*, F. Cuv.)," but larger, with longer feet and heavier muzzle. Thomas qualified, however, that the type of *elegans* is "a bleached and deteriorated skin and all the examples of the new form [*moreni*] being in spirit, it is impossible to compare them satisfactorily." Two specimens from Media Agua, San Juan, south of the type locality of *moreni* in Rioja, are like pale phase representatives of *typus*, on the one hand, and agree completely with the description and figure of *puerulus*, on the other. *Eligmodontia marica* Thomas is also pale and was first characterized as the smallest "species" of the genus. Of the four original specimens obtained by Budin, measurements of only the type of *marica* are given. The dimensions indicate either a juvenal or very small adult otherwise not distinguishable from other *Eligmodontia* within the range here assigned to *puerulus*. The pale *hirtipes* Thomas from the arid region about Lake Poopo was first described as a *Phyllotis* and compared with African jumping mice of the genus *Gerbillus*. Thomas described *jacunda* as a subspecies of *hirtipes* on the basis of its being "greyer and duller." Of two specimens at hand from Chorillos, Los Andes, south of the Jujuy type locality of *jacunda*, one is as pale, with tail nearly all white, the other is an ordinary dark phase individual with sharply bicolor tail.

Measurements.—See Table 8.

Specimens examined.—10. ARGENTINA.—*Los Andes:* Chorillos, 2 (MACN). *Catamarca:* Corral Quemado, 1 (CNHM). *San Juan:* Media Agua, 2 (AMNH). CHILE.—*Antofagasta:* Río San Pedro, 20 miles east of San Pedro, 5 (CNHM).

TABLE 2. —Measurements of *Calomys sorellus* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
Huamachuco[1]	72	62	19.5	17	22.7	10.7[2]	3.5
Otuzco	95	59	19	—	24.2	11.9	3.6
Macate	—	—	—	—	23.5	12.5	4.0
Tullparaju	107	73	21	18	25.6	13.0	4.0
Quilcayhuanca	98,92	72,66	20,19	18,17	24.4,23.7	12.3	3.7
Catac	94	68	20	20	24.1	12.6	3.7
Panao	87	75	17	—	—	—	3.7
Cullcui	94	80	19	—	24.3	12.6	3.6
Huánuco	82(77–91)8	70(65–75)8	17(16–18)8	—	23.1(22.0–24.8)7	11.9(11.0–12.5)7	3.6(3.4–3.8)7
La Quinua	82(75–96)6	63(60–66)6	19(18–20)6	—	23.0,23.8	11.7,12.5	3.8(3.6–9.0)4
Carhuamayo	92	—	19	—	23.1	12.1	3.5
La Oroya	107,75	—,—	20,18	—	23.9,22.6	12.8,11.8	3.8,3.7
Yana Mayo[3]	86	76	19	—	26.6[4]	11.2[4]	3.6
Yana Mayo[5]	88	70	18.5	—	—	—	—
Locroja	89,98,91,96	72,85,62,74	19,20,21,20	17,18,17,18	24.0,24.2,24.4,24.8	12.6,13.1,12.3,13.0	3.6,3.8,3.4,3.7
Huancavelica	91(81–101)13	75(68–84)13	20(20–21)13	18(15–19)13	24.3(23.1–25.4)12	12.6(12.2–13.1)13	3.7(3.5–3.9)13
Lircay	94(89–102)11	81(73–90)11	20.5(20–21)11	17.5(16–19)11	24.6(23.3–26.0)10	12.7(12.2–13.6)10	3.8(3.6–4.0)10
Tambo	92(86–98)10	76(70–80)10	20(19–21)10	18(17–20)10	24.5(23.7–25.7)9	12.6(12.0–13.3)10	3.8(3.6–4.0)10
Huanta	89,97,96,98	63,81,70,79	19,21,20,21	17,18,17,18	24.0,24.6,25.1,25.8	12.3,12.7,13.3,13.6	3.7,3.8,3.9,3.7
Ocros	89,92,88,91	75,77,77,75	21,20,21,21	16,17,18,17	24.1,24.4,24.6,24.8	12.5,12.5,12.8,12.2	4.1,3.7,3.9,3.6
Pajonal	89,83	82,82	20,21	19,17	24.1,24.6	12.6,12.0	3.8,3.9
Andahuaylas	89(83–100)14	80(74–90)14	21(21–22)14	18(17–19)14	24.3(23.2–25.6)14	12.5(11.7–13.3)14	3.8(3.5–4.2)14
Matara	95(89–102)9	88(91–94)7	21(20–22)9	—	25.0(23.2–25.8)8	13.1(12.6–13.6)8	3.8(3.7–4.0)8
Cusco	98(93–106)5	79(75–89)5	21(20–22)5	—	24.6(23.4–26.0)5	13.3(13.0–13.9)5	4.0(3.9–4.2)5
Chirapata	95	91	21	17.5	25.5	13.6	3.9
Chospioc[6]	102	91	19[7]	18	26.7	14.0	3.9
Urco	79(74–90)15	81(73–89)15	19.5(18–21)15	18.5(17–19)15	24.0(22.9–25.5)12	12.8(12.1–13.3)10	3.9(3.7–4.0)13

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[1] Type of *sorellus* Thomas, a subadult, from original description.

[2] Patently a wrong figure; Thomas gives 11.0 as width of braincase, which is always less than zygomatic breadth.

[3] Type of *miurus* Thomas, from original description.

[4] Possibly erroneous. [5] Cotype, skull damaged. [6] Type of *frida* Thomas, from original description. [7] Without claw.

TABLE 3.—Measurements of *Calomys laucha laucha* Olfers

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
PARAGUAY[1]							
Guachalla	65(57–76)10	48(42–54)10	14(13–15)10	—	19.7(19.3–20.0)8	10.8(10.6–10.9)8	3.2(3.0–3.3)8
URUGUAY							
Polanco	83	59	17.5	—	22.3	12.4	3.3
Averias	77	51	17.5	—	20.6	11.4	3.2
"	82	58	17	—	21.8	11.7	3.4
Maldonado[2]	78	49	17	—	21.3	11.6	—
ARGENTINA							
Maimara[3]	100	98	21[4]	16	26.0	13.8	3.6
"	80	85	20	14	22	11.6	3.7
"	83	70	20	15	23.3	12.1	3.7
Jujuy[5]	94	83	19[3]	15	24.5	13.4	3.5
Chumbicha	69	70	16	15	20.3	11.3	3.7
Yacanto[6]	85	74	16[3]	14	23.2	—	3.3
La Plata[7]	72	72	16.5[3]	13.5	21.0	11.3	3.4
Henderson	82(81–84)4	65(49–75)4	18(18–19)4	—	21.3(21.2–21.5)4	11.5(11.4–11.6)4	3.4(3.3–3.7)4
Torrecita[8]	89	48	15	—	20.5	11.7	3.3
"	75(64–84)11	64(45–72)11	17.6(15–19)11	—	20.3(19.4–21.4)12	10.8(10.1–11.7)12	3.3(3.2–3.6)12
Dorrego	78(74–83)6	75(71–82)6	18.5(18–19)6	—	21.2(20.7–22.1)3	11.5(11.1–12.0)3	3.6(3.5–3.7)3
Algarrobo	75	75	—	13	22.7	12.0	3.6
"	87	83	—	14	21.8	12.2	3.4
Bahia Blanca[9]	72	40	14	9	—	—	—
Chimpay	95(89–101)7	78(70–86)7	19(18–20)7	—	23.4(21.8–24.4)5	12.0(11.4–12.5)5	3.5(3.2–3.8)5
VENEZUELA							
Maturín	72(60–79)8	44(31–54)8	15(13–16)8	12(10–13)8	20.8(20.3–21.7)5	11.3(11.0–11.7)5	3.6(3.5–3.7)5
CURAÇAO[10]	49,—	41,—	12.5,—	—,—	18.6,17.5	10.8,9.4	2.8[12],2.8[12]
ARUBA[11]	55,45,44,43	—,—,38,35	—,—,12.5,11	—,—,8.5,8.5	19.4,16.7,—,—	10.6,9.5,9.4,—	2.8[12],2.8[12],3.0[12]

[1] Measurements of specimens described by Azara, given on page 154.

[2] Cotype of *bimaculatus* Waterhouse, external measurements of dry skin from Thomas (1884, Proc. Zool. Soc. London, **1884**: 454), cranial measurements from Gyldenstolpe (1932, K. Sv. Vet. Akad. Handl., **11**: 143).

[3] Type of *musculinus* Thomas, from original description. [4] Without claw. [5] Type of *cortensis* Thomas, from original description.

[6] Type of *cordovensis* Thomas, from original description. [7] Type of *murillus* Thomas, from original description.

[8] Type of *bonariensis* Osgood.

[9] Type of *gracilipes* Waterhouse, from original description; external measurements taken from dry skin.

[10] Type of *Baiomys hummelincki* Husson, followed by those of a paratype; measurements from original description; external measurements from the dry skin.

[11] External measurements of first two specimens from dry skins, of last two from specimens in alcohol.

TABLE 4.—Measurements of subspecies of *Calomys lepidus* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of upper molar row
lepidus							
PERU							
Carhuamayo	98,98	41,44	18,20	—,—	—,23.2	—,12.8	3.8,3.8
Junín[1]	77,71	—,38	17.8[2],17.7[2]	—,—	23.9,23.1	13.5,12.7	3.6,3.6
Santa Inéz	90	40	18	18	23.0	12.1	3.6
San Miguel	88	43	19	18	22.9	12.4	3.6
Lauramarca[3]	82[4]	46	17.7[2]	—	—	—	3.7
ducillus							
PERU							
Salinas	81(74–91)5	40(35–44)5	18.5(18–20)5	—	22.6(21.3–23.8)3	12.0(11.1–12.6)3	3.7(3.5–3.9)3
Huacullani	83,92	33,40	16,17	—,—	21.6,22.2	12.4,12.2	3.6,3.6
Yunguyo	85,89	45,44	18,19	—,—	22.7,—	12.4,13.0	3.4,3.7
Chucuito	84	39	18	—	22.8	12.1	3.8
Collacachi	80,86,79	38,40,37	17,18,17	—,—,—	22.7,23.1,23.8	12.4,12.4,12.5	3.8,3.7,3.8
Posoconi	76,83	39,43	17,17	—,—	21.9,22.0	11.8,11.6	3.5,3.6
carillus							
BOLIVIA							
Choro[5]	74	49	17[2]	17	21.5	11.4	3.4
Choro	73	45	16[2]	16	—	—	3.6
La Cumbre[6]	—	—	—	—	—	—	—
La Cumbre[7]	78	40	17	—	21.7	10.8	3.7
argurus							
ARGENTINA							
Abrapampa	79	45	16.5[2]	16.5	22	12	3.4

[1] Type and cotype of *lepidus* Thomas, from original description. [2] Without claw.

[3] Type of *marcarum* Thomas, from original description. [4] From dry skin.

[5] Type of *carillus* Thomas, from original description.

[6] Type of *montanus* Sanborn, a subadult, from original description. [7] Subadult.

TABLE 5.—Measurements of *Calomys callosus callosus* Rengger

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
BRAZIL							
Descalvados	113(103–126)4	80(74–87)4	21(21–22)4	—	27.3(26.1–29.1)4	14.8(13.9–16.0)3	4.3(4.0–4.5)4
Urucum	109,106,117	75,81,81	21,22,22	—	26.3,26.8,26.9	—,14.1,14.4	4.2,4.3,4.1
BOLIVIA							
Trinidad	122	78	23	—	27.7	14.8	4.2
Solacamo[1]	106	82	21	19	28.8	14.6	4.1
Ichilo	106,—	65,—	20,—	—,—	—,28.4	14.5,—	4.1,4.4
Buena Vista	98	73	20	—	25.6	—	4.1
Tacuara	—	—	—	—	26.2	—	4.5
S. Antonio[2]	89	69	20	16	25.3	13.2	4.1
Tablada[3]	124	90	21	18	29	15.5	4.6
Villa Montes	—	—	—	—	26.5	—	4.3
PARAGUAY							
Guachalla	100(82–120)6	80(68–90)6	22(19–25)6	—	26.0(24.7–27.0)3	13.6(13.1–14.0)4	4.4(4.2–4.6)4
Río Paraguay[4]	117	85.7	19.6	—	—	—	—
” ”	111(100–116)4	84(75–90)4	22(20–23)4	—	26.9(26.0–27.7)4	13.7(13.2–14.2)4	4.2(4.0–4.5)4
Goya[5]	115	77	21	18	29.2	16	4.5
ARGENTINA							
Aguaray	105,112,125	78,91,92	20,22,22	18,20,20	26.9,27.2,28.6	14.1,14.1,—	4.2,4.2,4.6
Santa María	114	88	22	18	28.6	15.2	4.1
Calilegua	114(92–137)10	83(72–100)10	22(21–25)10	—	27.0(24.9–29.6)9	14.3(13.4–15.4)9	4.4(4.1–4.9)9
Burruyacu	104	80	22	19	27.0	14.9	4.7
Tafi Viejo	88	65	20	17	25.8	—	4.3
Concepción	—	—	—	—	26.1(23.6–28.5)35	14.2(12.8–15.2)32	4.4(4.1–5.0)42
Cosquín[6]	94	72	21	16[7]	—	14.5	4.3

[1] Type of *boliviae* Thomas, from original description.

[2] Type of *muriculus* Thomas, from original description.

[3] Type of *fecundus* Thomas, from original description.

[4] Type of *callosus* Rengger, from original description.

[5] Type of *callidus* Thomas, from original description.

[6] Type of *venustus* Thomas, from original description.

[7] Dry.

TABLE 6.—Measurements of *Calomys callosus expulsus* Lund

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
BRAZIL							
Lagôa Santa[1]	96	80	19	—			
" " [1]	128[2]	76	20	—			
" " [1]	117[2]	74	20	—			
" " [1]	108	65	20	—			
" " [1]	100	67	19.5	—	—		
" " [1]	104	74	18	—	—	—	—
" " [1]	88	71	—	—	—	—	—
" " [3]	—	—	—	—	24.5	14.3	4.0
" " [1]	—	—	—	—	26.0	—	4.0
" " [1]	—	—	—	—	28.0	—	4.3
" " [4]	124	85	—	—	—		—
" " [5]	—	—	19.2	—	26.7	14.3	4.0
São Domingo	—	—	21	—	26[6]	13.7	4.1

[1] Cotypes, from Winge (1888, E. Mus. Lundii, **1**, no. 3: 17, 20–21).

[2] Said to be "overstretched."

[3] Skull figured by Winge (op. cit., pl. 2, fig. 4).

[4] "Type," from Gyldenstolpe (1932, K. Sv. Vet. Akad. Handl., (3), **11**: 143).

[5] Cotype, from Gyldenstolpe (op. cit.).

[6] Approximately.

TABLE 7.—Measurements of *Eligmodontia typus typus* F. Cuvier

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
ARGENTINA							
Buenos Aires[1]	68	90	20.3	—	—	—	—
” ”[2]	65	87	19.6	—	23.5	14.0	3.8
Peru Station[3]	75	80	20.4[4]	17	23.4	—	3.6
Bahía Blanca[5]	91	95	21.0[4]	—	—	—	—
Choele-Choel	90	87	25.0	17	26.1	13.3	3.9
” ”	90	107	24.0	18	24.9	13.0	4.0
” ”	81	108	21.0	18	23.9	12.0	4.0
Chos Malal	88	—	26.0	17	25.5	13.6	4.2
” ”	90	96	24.0	17	25.6	—	4.2
” ”	91	110	25.0	18	25.9	12.9	4.0
Las Lajas	92	102	22.0	17	25.3	—	4.1
Pilcaniyeu	76	78	21.0	16	24.0	—	4.1
Huanu Luan	92	87	23.0	—	24.9	12.3	3.8
Rawson	77	81	25.0	18	23.8	—	—
Bas. Canyons[6]	85	80	23.0[4]	13[7]	24.0	12.0	4.0[8]
Piedra Clavada	80	72	22.0	15	—	11.8	3.7
Río Coyle	—	—	—	—	—	12.5	4.1
C. Buen Tiempo	—	—	—	—	23.8	12.3	3.5
Santa Cruz	70	72	23.0	—	23.3	11.6	3.7
” ”	68	69	23.0	—	23.0	11.4	3.5
CHILE							
L. Sarmiento	83	70	23.0	—	23.0	12.0	3.9

[1] Type of *typus* Cuvier, from original description (Old French inches converted to millimeters=1″ : 27.07 mm.).

[2] Type of *typus* Cuvier, from Gyldenstolpe (1932, K. Sv. Vet. Akad. Handl., **2**: 142).

[3] Type of *pamparum* Thomas, from original description.

[4] Without claw.

[5] Type of *elegans* Waterhouse, from original description.

[6] Type of *morgani* J. A. Allen, from original description.

[7] From dry skin.

[8] 3.5 mm., according to Goodwin (1953, Bull. Amer. Mus. Nat. Hist., **102**: 323).

TABLE 8.—Measurements of *Eligmodontia typus puerulus* Philippi

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
BOLIVIA							
Challapata[1]	90	97	25.0[6]	20	25.3	13.5	3.8
CHILE							
Tarapaca[2]	93	67	22.0	22	—	—	—
Río S. Pedro	87	88	23.5[7]	—	25.2	13.0	3.7
" " "	78	79	23.5[7]	—	—	—	—
" " "	92	95	24.0[7]	—	25.9	13.8	4.1
" " "	97	93	26.0[7]	—	25.6	13.7	3.9
" " "	105	88	24.0[7]	—	—	—	—
S. Pedro Atacama[3]	90	70	21.0[6]	—	—	—	—
ARGENTINA							
Abrapampa[4]	85	80	22.0[6]	18	25.0	13.2	4.0
Chorillos	88	89	22.0	16	—	—	—
"	84	81	23.0	18	—	—	—
Chumbicha[5]	65	93	20.0[6]	15	21.4	12.0	3.5
Corral Quemado	70	76	22.0[7]	15	22.7	11.7	4.0
Chilecito[8]	80	91	23.0[6]	17	—	12.4	3.6
Media Agua	81	89	21.0	15	—	—	—
" "	70	85	20.0	15	—	—	—

[1] Type of *hirtipes* Thomas, from original description.

[2] Type of *tarapacensis* Mann, from original description.

[3] Type of *puerulus*, from original description.

[4] Type of *jacunda* Thomas, from original description.

[5] Type of *marica* Thomas, from original description.

[6] Without claw.

[7] Dry, with claw.

[8] Type of *moreni* Thomas, in spirits, from original description.

Genus **Zygodontomys** J. A. Allen

Zygodontomys J. A. Allen, 1897, Bull. Amer. Mus. Nat. Hist., **9**: 38, pl. 1, figs. 1-7 (skull, molars).

Type species.—Oryzomys cherriei J. A. Allen (=*Zygodontomys brevicauda cherriei* J. A. Allen).

Included species.—Zygodontomys lasiurus Wagner, *brevicauda* J. A. Allen and Chapman.

Distribution

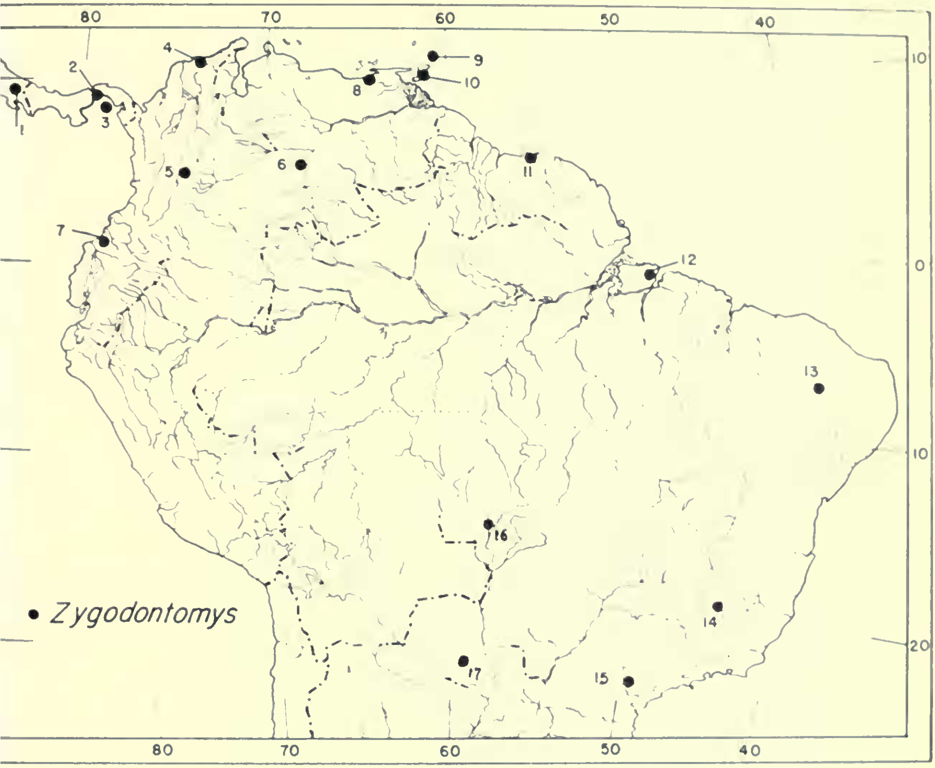
Figure 50

Tropical savannas, brushlands, and forest fringes from Costa Rica southward into Colombia, western Ecuador, Venezuela, the Guianas, eastern Brazil and the Mato Grosso, Paraguay and northeastern Bolivia; altitudinal range from sea level to approximately 1200 meters above.

Characters

External.—Largest member of the *Calomys* group; form and appearance *Sigmodon*-like; pelage smoothly adpressed, the cover hairs slightly hispid; upper parts and sides buff to tawny mixed with blackish with a resultant agouti pattern; under parts not sharply defined from sides, gray usually washed with buff; tail shorter to slightly longer than combined head and body length, thinly haired, without terminal tuft, brown above, paler beneath except terminally; hind feet comparatively large, brown or buffy above, soles relatively well scutulated, plantar surface of heel pilose, claws strongly developed but length of middle claw measured on ventral surface not exceeding one-half length of its digit, digital bristles sparse; fifth hind toe, less claw, not reaching distal end of first phalanx of fourth toe; ears small, about one-third shorter, measured from notch, than hind foot with claw; auricular patches or tufts not present; mammae, $2-2=8$.

Cranial (figs. 34, 51, 66).—Skull comparatively heavily built, braincase relatively narrow; zygomata parallel-sided or convergent anteriorly, widest distance between them less than length from posterior tips of nasals to anterior border of supraoccipital; supraorbital region broad, the dorsal surface convex in cross section, width at mid-frontal region more than greatest width of rostrum, sides divergent, the edges beaded and, sometimes, projected laterally as narrow ledges; temporal ridges often present; greatest dis-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● Zygodontomys

FIG. 50.—Type localities of the nominal subspecies of *Zygodontomys brevicauda* and *Z. iurus*.

EXPLANATION OF FIGURE 50

Zygodontomys brevicauda cherriei

1. Boruca, near Río Diquis, Puntarenas, Costa Rica.

Zygodontomys brevicauda ventriosus

2. Tabernilla, Canal Zone, Panamá.

Zygodontomys brevicauda seorsus

3. San Miguel Island (Isla del Rey), Archipielago de las Perlas, Golfo de Panamá, Panamá.

Zygodontomys brevicauda sanctaemartae

4. Bonda, Santa Marta, Magdalena, Colombia.

Zygodontomys brevicauda brunneus

5. El Saibal, Cundinamarca.

Explanation of Figure 50 (*continued*)

Zygodontomys brevicauda stellae

6. Maipures, Vichada, Colombia.

Zygodontomys brevicauda punctulatus

7. Western Ecuador (see text).

Zygodontomys brevicauda thomasi

8. Campo Alegre, Cumaná, Sucre, Venezuela.

Zygodontomys lasiurus tobagi [=*Z. b. brevicauda?*]

9. Tobago, West Indies.

Zygodontomys brevicauda brevicauda

10. Princestown, Trinidad.

Zygodontomys brevicauda microtinus

11. Suriname.

Zygodontomys lasiurus fuscinus

12. Soure, Ilha de Marajó, Pará, Brazil.

Zygodontomys lasiurus pixuna

13. Crato, Ceará, Brazil.

Zygodontomys lasiurus lasiurus

14. Lagôa Santa, Rio das Velhas, Minas Gerais, Brazil.

Zygodontomys lasiurus brachyurus

15. Itararé, São Paulo, Brazil.

Zygodontomys [*?lasiurus*] *lenguarum*

16. Waikthlatingmayaliva, northern Chaco, Paraguay.

Zygodontomys [*?lasiurus*] *tapirapoanus*

17. Tapirapoã, Rio Sepotuba, Mato Grosso, Brazil.

tance across fronto-maxillary sutures on dorsal surface subequal to distance from anterior border of supraoccipital to angle between fronto-parietal sutures; fronto-parietal sutures crescentic or broadly angular in outline, never forming a right or acute angle at midline; interparietal moderately well developed to notably reduced antero-posteriorly; anterior border of zygomatic plate plane or slightly concave, the upper corner rounded or pointed; posterior border of incisive foramina pointed or rounded and sometimes, in old individuals, not extending behind to anterior plane of first molars; pitted posterior palatal region usually without median longitudinal ridge, lateral depressions present or absent, posterior border rounded, angular, square, or with a blunt median projection; width of mesopterygoid fossa at anterior base of pterygoid processes equal to or greater than width of parapterygoid fossa measured at same plane; bullae small, their length, less tubes, equal to or less than alveolar length of molar row; coronoid process well developed and at least one-half as long as condylar process.

Dental (figs. 44, 49).—Upper incisors opisthodont, ungrooved; molar rows parallel-sided or slightly convergent posteriorly; molars moderately high-crowned, crested in unworn, secondarily terraced in worn; individual cusps of upper and lower molars ovate in outline, those of inner side opposite their analogues of outer side; upper first molar three or four rooted, the lower two or three rooted; m_3 from three fourths to equal the length of m_2; procingulum of m_1 subelliptical or subcordate in outline, an anterior median fold, if present, never more than a notch in adult, sometimes moderately developed in juvenal; $m^{1\,2}$ with well-developed anterolabial style present, the first primary fold becoming an island in moderately worn tooth; second secondary fold present in unworn, sometimes in slightly worn, $m^{1\,3}$; first minor fold weakly developed and virtually absent in moderately worn $m^{2\,3}$; a vestigial mesoloph sometimes present in juvenal m^3; procingulum of $m_{2\,3}$ rudimentary, absent in worn teeth; second primary fold reduced to a small shallow enamel island in moderately worn $m_{1\,2}$, obsolete in slightly worn m_3; a paralophule and mesostyle often present, sometimes fused and bridging paracone and metacone.

Comparisons

Zygodontomys is distinguished from *Calomys callosus*, its nearest relative, by larger size throughout, mesopterygoid fossa broader, dorsal emargination of antorbital foramen shallower, incisive for-

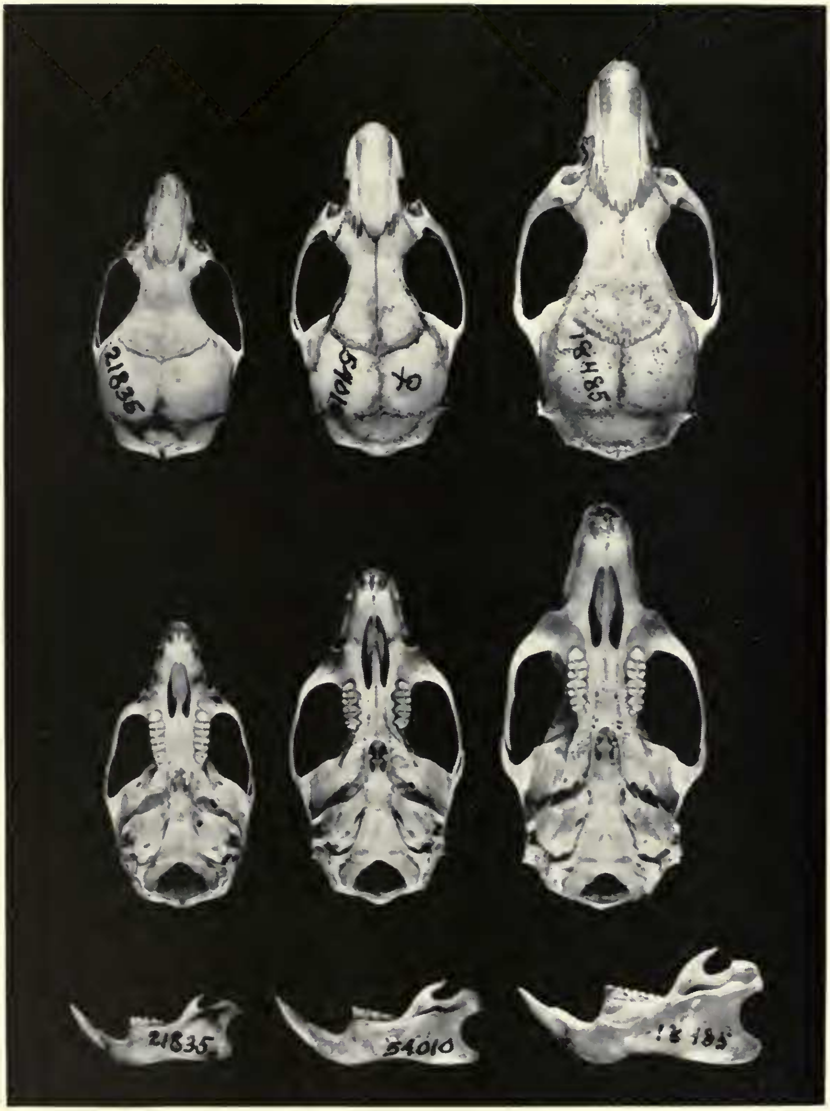
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FIG. 51.—*Zygodontomys brevicauda.* Dorsal and palatal aspects of skull and mandibles to show variation in size (slightly more than ×1½).

amina wider, cusps more ovate and generally opposed in position, third lower molar not shorter than second. Other members of the *Calomys* group are much smaller and more divergent in external cranial and dental characters. In the case of skulls only with molars worn flat, the above cranial and dental characters for distinguishing *Zygodontomys* from *Calomys callosus* serve also to separate the former from *Phyllotis griseoflavus*. In addition, first minor fold of adult $m_{\overline{2}-\overline{3}}$ is reduced or obsolete in *Zygodontomys* as compared with the same folds in *Phyllotis griseoflavus* (fig. 44).

Zygodontomys is distinguished from *Pseudoryzomys* chiefly by its generally vole-like shape, larger size, relatively shorter tail, smaller hind foot, broader and distinctly inflated frontal region; crowns of molars crested, cusps of inner and outer sides very nearly opposite each other, not arranged in echelon (cf. figs. 44 and 56).

Dark representatives of *Zygodontomys* closely resemble the reddish brown *Akodon aerosus* Thomas (*A. dayi* Osgood a synonym) and the Trinidad *A. urichi* J. A. Allen and Chapman. The skulls are also similar except that the anterior zygomatic plate is but slightly produced forward as seen from above, and in *A. aerosus* supraorbital ridges or beading is absent. In both species of *Akodon* the molars are more hypsodont; the second molars, upper and lower, are markedly longer than wide; the first and second upper primary folds form an echelon file with the folds of the opposite side, and after moderate wear tend to disappear altogether from the crown surface. Other but not all nominal species of *Akodon* may be distinguished from *Zygodontomys* by one or more of the following characters: proodont upper incisors; unridged and parallel- or concave-sided interorbital region; weak anterior zygomatic plate; smaller interparietal; nasals produced anteriorly to form a trumpet or produced posteriorly well behind the fronto-maxillary suture; middle claw of forefoot more than one-half the length of its digit. Each of these characters is less than generic and some may vary individually and geographically. No sharp line can be drawn between *Zygodontomys* and the nominal species *Akodon varius* Thomas, *A. arviculoides* Wagner and *A. obscurus* Waterhouse.

Zygodontomys has sometimes been confused with *Oryzomys* (*Melanomys*) *caliginosus*. The mesolophodont molar pattern and fine, but trenchant, differences in cranial structure, especially in the palatal region of the latter, readily separate it from the former. *Oryzomys caliginosus*, a vole-like forest dweller, may be replaced by *Zygodontomys* where deforestation exposes the one and permits the introduction of the other.

Remarks

Zygodontomys has been confused with oryzomyine and akodont rodents. Resemblance to *Oryzomys,* notably *O. caliginosus,* is a case of parallel development of ecological counterparts, one a grass- and scrubland vole, the other a forest vole. True *Akodon,* however, like *Zygodontomys,* is a grass- and scrubland vole and resemblance between the two genera indicates close genetic relationship rather than convergence. Indeed, *Zygodontomys* is an annectant form between phyllotine and akodont rodents. Cranial characters of *Zygodontomys* combine features of both groups. The high braincase, well-inflated frontal sinuses, reduced interparietal, posteriorly narrowed incisive foramina and shorter than usual palate in many specimens of *Zygodontomys,* are definitely akodont characters. The molar pattern of *Zygodontomys* is less modified than that of *Akodon* proper but represents a stage in the line leading to the highly selenodont molars of the Central American akodont genus *Scotinomys.* Further clarification of the status of *Zygodontomys* requires a reassessment of the systematics of akodont rodents comparable to the present one of phyllotines.

The following account and arrangement of the species and subspecies of *Zygodontomys* are typologically based.

The Species

Twenty named forms of *Zygodontomys* are taken into account here. Types of sixteen of these were examined by me and found to be conspecific. Of the four types not seen, the first, *Zygodontomys lasiurus* Lund, is known to me by a paratype in the British Museum (Natural History) and the original description and figures. The second, *pixuna* Moojen, from Ceará, Brazil, was originally distinguished from topotypes of *Zygodontomys lasiurus* by paler color and more slender skull. Material from Ceará and Piauhy in the collection of Chicago Natural History Museum shows that specific status first accorded *pixuna* is untenable, and subspecific separation from *lasiurus* is doubtful. The third named form, *brachyurus,* is here identified as a *Zygodontomys* solely on evidence from the literature. There is nothing to indicate specific distinction from *Z. lasiurus.* The fourth named form, *Zygodontomys seorsus* Bangs, from San Miguel Island, Panamá, is represented here by six paratypes. They average larger than populations of *Zygodontomys brevicauda* from Trinidad, Panamá and northern Colombia, but otherwise are practically indistinguishable.

Oryzomys obtusirostris J. A. Allen, 1900, subsequently referred by its author to *Zygodontomys*, is a true *Oryzomys*.

Specimens of *Zygodontomys* at hand segregate into two geographic groups. Each of these is provisionally accorded specific rank. The first or northern group, typified by *Z. brevicauda*, ranges from north of the Rio Amazonas into Central America. It is characterized by widely opened, ovate incisive foramina, longer palate, prominently pitted posterolateral palatal depressions, posterior border of palate with either a rounded or lancet-shaped excision, mesopterygoid fossa extremely wide, interparietal well developed antero-posteriorly, capsular projection of mandible usually located at base of coronoid process, upper incisors opisthodont. The type species of the southern group, *Zygodontomys lasiurus*, occupies suitable habitats in Brazil south of the Amazonas. It is distinguished by incisive foramina usually narrower posteriorly than anteriorly, palate shorter, the posterior border commonly with a short blunt median process, posterolateral palatal pits generally situated posteriad to hind border of palate, mesopterygoid fossa narrower relative to intermolar width of palate, interparietal reduced antero-posteriorly, capsular projection of mandible usually located posteriad to base of coronoid proccess, upper incisors opisthodont to practically orthodont. Many juvenals and subadults of the northern group are intermediate and, sometimes, more nearly like adults of the southern group.

Recognition of the subspecies listed below is uncritical.

Measurements of the types of each of the named forms of *Zygodontomys* are given in Table 9.

Since the present review was written and submitted for publication (prior to 1957), Cabrera's (1961, p. 462) classification of *Zygodontomys* has come to hand (March, 1962). This authority recognizes four species. His *Z. lasiurus* agrees with mine but his *microtinus*, *punctulatus* and *brevicauda* are treated below as subspecies of the last-named form.

NORTHERN GROUP

Zygodontomys brevicauda cherriei J. A. Allen

Oryzomys cherriei J. A. Allen, 1895, Bull. Amer. Mus. Nat. Hist., 7: 329.

Type locality.—Boruca, near Río Diquis, Puntarenas, Costa Rica.

Remarks.—Three paratypes, received in exchange, are in the collection of Chicago Natural History Musuem.

Zygodontomys brevicauda ventriosus Goldman

Zygodontomys cherriei ventriosus Goldman, 1912, Smithsonian Misc. Coll., **56**, No. 36: 8.

Type locality.—Tabernilla, Canal Zone, Panamá.

Remarks.—Two paratypes, received in exchange, are in the collection of Chicago Natural History Museum.

Zygodontomys brevicauda seorsus Bangs

Zygodontomys seorsus Bangs, 1901, American Nat., **35**: 642.

Type locality.—San Miguel Island [Isla del Rey], Archipielago de las Perlas, Golfo de Panamá, Panamá.

Remarks.—Six paratypes, received in exchange, are in the collection of Chicago Natural History Museum.

Zygodontomys brevicauda sanctaemartae J. A. Allen

Oryzomys sanctaemartae J. A. Allen, 1899, Bull. Amer. Mus. Nat. Hist., **12**: 207.

Type locality.—Bonda, Santa Marta region, Magdalena, Colombia.

Remarks.—Doubtfully separable from *brunneus* Thomas. See remarks under *Z. b. brunneus.*

Zygodontomys brevicauda brunneus Thomas

Zygodontomys brunneus Thomas, 1898, Ann. Mag. Nat. Hist., (7), **2**: 269.

Zygodontomys griseus J. A. Allen, 1913, Bull. Amer. Mus. Nat. Hist., **32**: 599—type locality, El Triumfo, Magdalena Valley, Colombia, 600 ft. above sea level [about latitude of La Dorada].

Zygodontomys fraterculus J. A. Allen, 1913, Bull. Amer. Mus. Nat. Hist., **32**: 599—type locality, Chicoral, Río Coello, Magdalena Valley, Tolima, Colombia, altitude, 1800 ft. above sea level.

Type locality.—El Saibal, Magdalena Valley, Cundinamarca, Colombia.

Remarks.—The *Zygodontomys* collected by the writer in Colombia represent all forms, except *stellae,* described from that country. This material and field observations will form the basis for a more detailed account of the genus.

Zygodontomys brevicauda punctulatus Thomas

[?]*Hesperomys renggeri,* Tomes (nec Waterhouse), 1860, Proc. Zool. Soc. London, **1860**: 213—Ecuador (without precise locality).

Hesperomys arvicoloides, Tomes (nec Pictet), 1860, Proc. Zool. Soc. London, **1860**: 262—Ecuador (without precise locality).

Acodon [sic] *punctulatus* Thomas, 1894, Ann. Mag. Nat. Hist., (6), **14**: 361.

Type locality.—"Ecuador (probably Pallatanga)," but if Ecuador is the country of origin it is much more likely that the type was taken in the lowlands of western Ecuador as indicated on the map (fig. 50).

Remarks.—To date, *punctulatus* is known only from the type.

Zygodontomys brevicauda stellae Thomas

Zygodontomys stellae Thomas, 1899, Ann. Mag. Nat. Hist., (7), **4**: 380.

Type locality.—Maipures, upper Río Orinoco, Vichada, Colombia.

Zygodontomys brevicauda thomasi J. A. Allen

Zygodontomys thomasi J. A. Allen, 1901, Bull. Amer. Mus. Nat. Hist., **14**: 39.

Type locality.—Campo Alegre, Cumaná, Sucre, Venezuela.

Remarks.—Doubtfully distinct from *brevicauda.*

Zygodontomys brevicauda brevicauda J. A. Allen and Chapman

Oryzomys brevicauda J. A. Allen and Chapman, 1893, Bull. Amer. Mus. Nat. Hist., **5**: 215.

Akodon frustrator, J. A. Allen and Chapman, 1897, Bull. Amer. Mus. Nat. Hist., **9**: 20—type locality, Caura, Trinidad.

Zygodontomys brevicauda tobagi[1] Thomas, 1900, Ann. Mag. Nat. Hist., (7), **5**: 274—type locality, Island of Tobago, British West Indies.

Type locality.—Princestown, Trinidad.

Remarks.—Three paratypes of *brevicauda* and one of *frustrator*, received in exchange, are in the collection of Chicago Natural History Museum.

Zygodontomys brevicauda microtinus Thomas

Oryzomys microtinus Thomas, 1894, Ann. Mag. Nat. Hist., (6), **14**: 358.

Type locality.—Suriname.

SOUTHERN GROUP

Zygodontomys lasiurus fuscinus Thomas

Akodon fuscinus Thomas, 1897, Ann. Mag. Nat. Hist., (6), **19**: 496.

Type locality.—Soure, Ilha de Marajó, mouth of Amazon, Pará, Brazil.

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[1] Goodwin (1962, Amer. Mus. Nat. Hist., Novit., no. 2096, p. 7) recognizes *Zygodontomys brevicauda tobago* [sic] as a distinct race larger than Trinidad *brevicauda.*

Zygodontomys lasiurus pixuna Moojen

Zygodontomys pixuna Moojen, 1943, Bol. Mus. Nac., Rio de Janeiro, Zool., no. 5: 8, fig. 2 (skull and molars).

Type locality.—Crato, Ceará, Brazil.

Zygodontomys lasiurus lasiurus Lund

Mus lasiurus Lund, 1839, Ann. Sci. Nat., Paris, **11**: 233 (nomen nudum). Lund, 1840, Mag. Nat. Hist., new ser., **4**: 55 (description inadequate). Lund, 1841, K. Danske Vidensk. Selsk. Afhandl., **8**: 50–52, 134, 266, 280, 294.

Habrothrix lasiurus, Winge, 1888, E Mus. Lundii, **1**, pt. 3: 31, pl. 1, fig. 8 (head), fig. 9, (hind foot), pl. 2, fig. 11 (skull), fig. 11*a* (molar).

[*Zygodontomys*] *lasiurus*, Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9**: 61.

Type locality.—Lagôa Santa, Rio das Velhas, Minas Gerais, Brazil.

Remarks.—Ellerman (1941, pp. 417, 418) regards *lasiurus* as "probably a member of the genus *Akodon.*" More probable, in my opinion, is that a number of species in the British Museum referred by Thomas to *Akodon* should have been determined as *Zygodontomys lasiurus.* One of the types in the Copenhagen Museum is described and figured by Winge (supra cit.). Another specimen of the original type series, collected by Reinhardt in Lagôa Santa, is in the British Museum (BM No. 88.1.9.4).

Zygodontomys lasiurus brachyurus Wagner

Hesperomys brachyurus Wagner, 1845, Arch. Naturg., **11**: 147. Wagner, 1848, Abh. K. Akad. München, **5**: 313. Pelzeln, 1883, K. K. Zool.-Bot. Gesellsch., Beih., **33**: 70.

Akodon sp. Thomas, 1901, Ann. Mag. Nat. Hist., (7), **8**: 530—Rio Jordão, Minas Gerais, Brazil.

[*Zygodontomys*] *brachyurus*, Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9**: 61 (closely allied to *Mus lasiurus*).

Zygodontomys lasiurus, Vieira, 1955, Arq. Zool., São Paulo, **8**: 146—Ipiranga and Piracicaba, São Paulo, Brazil.

Type locality.—Itararé, São Paulo, Brazil.

Zygodontomys [? **lasiurus**] **lenguarum** Thomas

Akodon lenguarum Thomas, 1898, Ann. Mag. Nat. Hist., (7), **2**: 271.

Type locality.—Waikthlatingmayaliva, northern Chaco, Paraguay.

Remarks.—The dividing line between this, the following (*tapirapoanus*), and *Akodon obscurus* Waterhouse from Uruguay, is not clear.

Zygodontomys [? lasiurus] tapirapoanus J. A. Allen

Zygodontomys tapirapoanus J. A. Allen, 1916, Bull. Amer. Mus. Nat. Hist., **35**: 528.

Type locality.—Tapirapoã, Rio Sepotuba, Mato Grosso, Brazil.

Remarks.—Specimens of *Zygodontomys* from Buena Vista, Santa Cruz, Bolivia, in the British Museum (Natural History), are referable to *tapirapoanus*.

TABLE 9.—Measurements of nominal subspecies of *Zygodontomys lasiurus* Lund and *Zygodontomys brevicauda* J. A. Allen and Chapman

(Measurements are of the type specimens unless otherwise indicated.)

Name	Sex	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
brachyurus	♂	133	63	24[8]	13	—	—	—
brevicauda	♂	—	—	—	—	32.5	17.3	4.5[1]
brunneus	♀	152	117c	25[2,8]	19[2]	34.0[3]	17.7[3]	5.0[3]
cherriei	♂	—	—	—	—	30.0	16.0	4.6
fraterculus	♀	115	83	26[2]	—	28.0	13.5	4.0[1]
frustrator	—	168	65	26	10[2]	26.0	13.0	4.5
fuscinus	♂	98[4]	64[4]	19[4,8]	13[4]	—	14.9	4.5
griseus	♂	133	101	26	—	28.5	14.0	4.2
lenguarum	—	115	76	21[8]	14	28.5	16.0	4.7[5]
lasiurus	—	121	74	21[8]	—	27.0[5]	—	4.8[5]
microtinus	♀	115[4]	84[4]	24.5[4,8]	16[4]	29.7	16.0	4.1
pixuna	♀	86[6]	120[6]	24.0	—	28.4	15.0	4.6
punctulatus	—	132	71	22.0[2,8]	14[2]	29.6	15.0	4.2
sanctaemartae	♀	129	100	27.0	15[2]	34.0	17.7	5.0
scorsus	♂	180	140	34.0	18	32.8	18.4	5.2
stellae	♂	110	38[7]	20.6[8]	17.7	30.0	15.0	4.2
tapirapoanus	♀	130	80	25	—	29.5	15.8	5.0
thomasi	♀	125	99	23	18	—	16.0	4.0
tobagi	♂	146	100	30[8]	18	35.0	19.0	4.6
ventriosus	♂	136	104	28	—	31.7	16.4	4.6

[1] Crown length; measuring points of molar row in others unknown.

[2] On dry skin.

[3] Of cotype.

[4] Of type in spirits.

[5] Of cotype, from Gyldenstolpe (1932, K. Sv. Vet. Akad. Handl., 2: 147).

[6] Head and body and tail measurements apparently reversed; Moojen gives head and body 112.5 and tail 80.5 as average for 10 adult female cotypes.

[7] Bob.

[8] Without claw.

PHYLLOTIS SECTION

The characters of the section are given in the key (p. 118). For the geographic range, see maps (figs. 1 and 52).

Genus **Pseudoryzomys** Hershkovitz

Pseudoryzomys Hershkovitz, 1959, Proc. Biol. Soc. Washington, **72**: 8.

Type species.—Oryzomys wavrini Thomas, by original designation.

Included species.—Pseudoryzomys wavrini Thomas.

Distribution

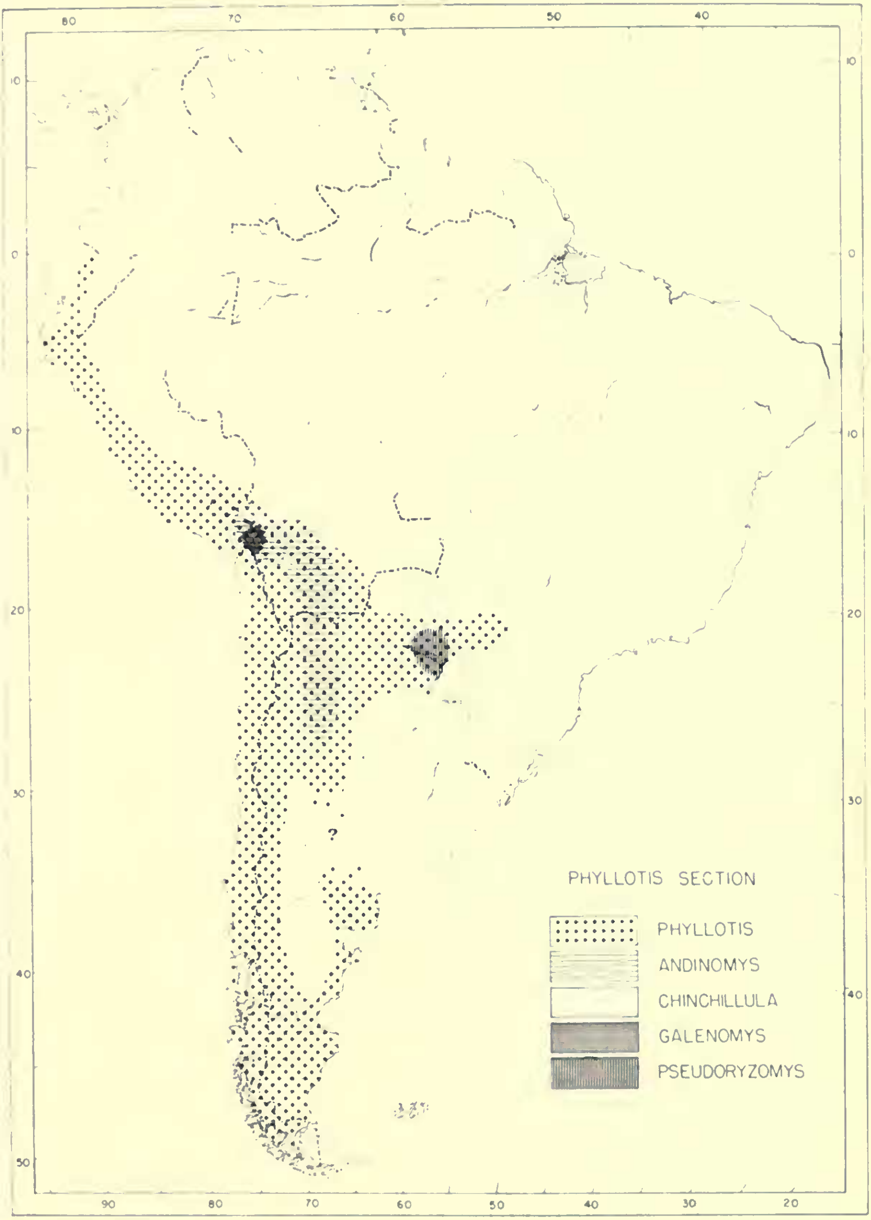
Figure 52

Known only from the Chaco of Paraguay and Argentina.

Characters

External.—Form and appearance as in palustrine and semiaquatic cricetines; pelage long, comparatively coarse, and loose but not lax; upper parts from snout to base of tail dark brown mixed with buffy, the dark basal portion of the hairs showing through; tail subequal to combined head and body length; thinly haired, without terminal tuft, brown above, paler beneath; hind foot comparatively large, average length, with claw, more than 22 per cent of combined head and body length; soles, including plantar surface of heel, well scutulated and entirely bare; webbing between middle digits of hind foot comparatively well developed, membrane between digits 3 and 4 extending to distal ends of first phalanges (fig. 53); claws weak, digital tufts thin; first hind toe, less claw, not extending to base of second; fifth hind toe, less claw, not reaching distal end of first phalanx of fourth toe; ears small, about one third shorter, measured from notch, than hind foot with claw; fifth (outer posterior) postdigital plantar pad obsolete or absent.

Cranial (figs. 54,*a*, 55,*a*).—Skull elongated, especially in frontal region, *zygomatic* arches parallel-sided, widest distance between them subequal to, or less than length from posterior tips of nasal to anterior


80
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PHYLLOTIS SECTION
PHYLLOTIS
ANDINOMYS
CHINCHILLULA
GALENOMYS
PSEUDORYZOMYS

FIG. 52.—Distribution of the genera of the *Phyllotis* section.

border of interparietal (not supraoccipital, the point used for measuring in all other phyllotines); supraorbital region narrow mid-frontally, the dorsal surface flat or concave in cross section, width at mid-frontal plane less than greatest width of rostrum, sides divergent, the edges beaded and continuing on parietals as temporal ridges; greatest distance across fronto-maxillary sutures on dorsal surface subequal to distance from anterior border of interparietal to angle between fronto-parietal sutures; fronto-parietal sutures crescentic, not forming a right or acute angle at midline; interparietal well developed; anterior border of zygomatic plate deeply concave, the upper corner pointed; incisive foramina narrow, their posterior borders extending behind anterior plane of first molars; palate hardly as wide between first molars as greatest length of m^1; paired anterior palatal pits situated across maxillo-palatal suture on middle of palatal bridge; posterior palatal region with a low median ridge, lateral depressions present; width of mesopterygoid fossa at base of hamular processes equal to or greater than width of parapterygoid fossa measured at same plane; length of bulla, less tube, subequal to alveolar length of molar row; coronoid process well developed, at least one-half as long as condylar process.

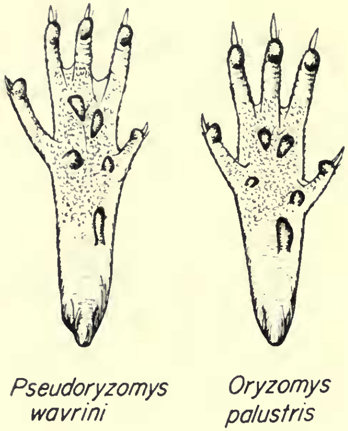


FIG. 53.—Plantar surface of right hind foot of *Pseudoryzomys wavrini* and *Oryzomys palustris*.

Dental (fig. 56,*a*).—Upper incisors opisthodont, ungrooved; molar rows parallel-sided; first upper and lower molars four-rooted; m_3 as long as, or longer than, m_2; molars moderately high crowned, terraced in unworn condition and tending to lamination in the upper, triangulation in the lower; individual cusps arranged nearly in echelon, compressed antero-posteriorly, the upper elliptical in outline, the lower subtriangular; procingulum of m^{1} elliptical in outline and distinctly biconulate in unworn condition, of m_{1} subtriangular, without anterior fold; mesolophs weakly developed or absent, mesolophid absent; a poorly developed mesostyle(-id) may be present in m^{1}; first primary fold, with corresponding anterolophs, of m^{2-3} well developed in unworn teeth; second secondary folds present as small enamel islands in unworn m^{1-3}; first internal folds of m^{2-3} not discrete but recognizable; first minor fold weakly developed in unworn to moderately worn m^{2}, obsolete in m^{3}; procingulum of m_{2-3} weakly developed; second primary fold well developed in moderately worn m_{1-3}; first minor fold present in m_{2-3}.

Comparisons

The combination of characters that distinguish *Pseudoryzomys* as a genus from all other phyllotines includes moderate size, small ears, large hind feet, soles entirely naked and with five plantar tubercles, webbing between toes well developed, unspecialized tail subequal to combined head and body length, zygomatic spread extremely narrow relative to skull length, interorbital region narrow with divergent and beaded supraorbital edges.

Pseudoryzomys is treated as a member of the *Phyllotis* section because of its terraced molars. In most other respects it appears to be more nearly related to members of the *Calomys* section. Cranially, it combines the narrow interorbital region characteristic of most phyllotines and the divergent and beaded supraorbital edges of *Zygodontomys*, *Calomys callosus* and *Phyllotis griseoflavus.* This combination occurs in no other phyllotine but is nearly approached in *Phyllotis darwini wolffsohni.*

Pseudoryzomys most nearly resembles *Zygodontomys* and *Calomys callosus* in size, pilosity of tail, and texture and color of pelage. The hind foot of *Zygodontomys,* however, is not specially adapted for natation, is smaller, more hairy, provided with stronger claws but with weaker interdigital webbing. Furthermore, *Zygodontomys* is larger, with tail relatively shorter, pelage finer, thicker, shorter, color of upper surface and sides of head and body more uniform and evenly ticked. *Calomys callosus* is approximately the same bulk as *Pseudoryzomys* but its tail is shorter, feet smaller, hirsute, comparatively delicate in structure, and without interdigital webbing.

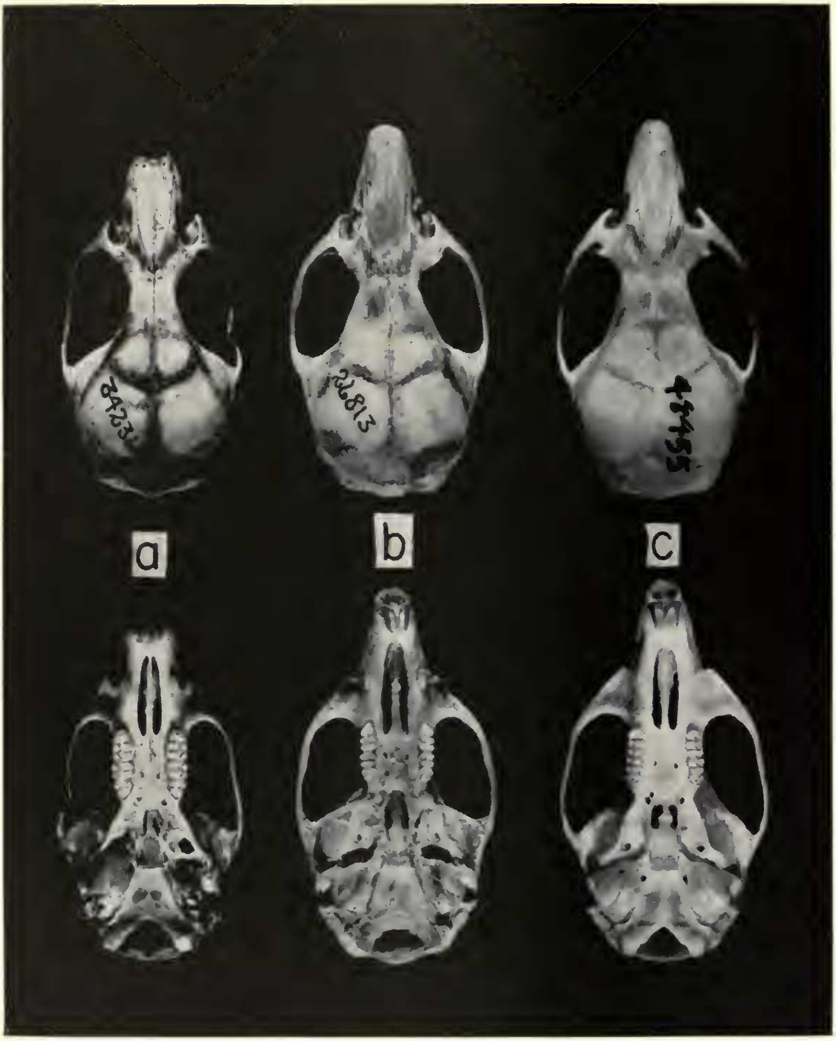


FIG. 54.—Dorsal and palatal aspects of skulls of *a*, *Pseudoryzomys wavrini* (with nasal tips missing); *b*, *Calomys callosus; c*, *Oryzomys palustris*. (About × 1½).

Texture and color of pelage in both *Zygodontomys* and *Calomys* are more nearly as in *Oryzomys* than *Pseudoryzomys*. In neither *Zygodontomys* nor *Calomys* is the antorbital foramen as deeply excised or the anterior border of the zygomatic plate as deeply concave.

Resemblances between *Pseudoryzomys* and palustrine species of *Oryzomys* (figs. 53–55) are of a convergent nature. The hind feet of

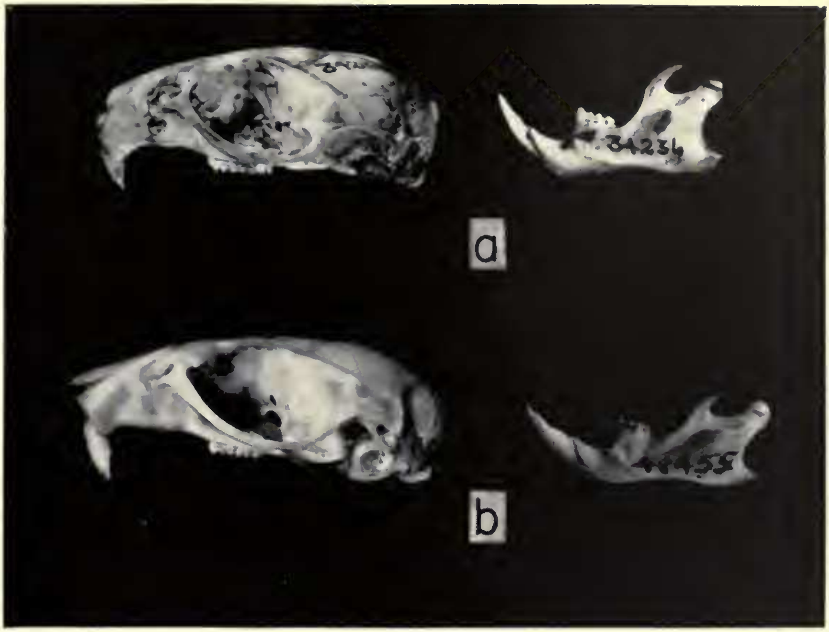


FIG. 55.—Side view of skull and mandible of *a*, *Pseudoryzomys wavrini* (with nasal tips missing); *b*, *Oryzomys palustris*. (About × $1\frac{1}{2}$.)

Pseudoryzomys, larger and more powerfully developed than in any other phyllotine, are like those of *Oryzomys palustris*. The wholly bare soles and well-developed interdigital webbing are also characters of *Oryzomys* and particularly of the oryzomyine *Nectomys*, rather than of phyllotines. These external characters, nevertheless, occur in nearly every murid more or less adapted for aquatic life. The long palate with posterolateral pits common to phyllotines and oryzomyines is narrower in *Pseudoryzomys* than in any oryzomyine. The hypsodont molars, advanced stages of lamination and triangulation of the crowns and cusps respectively, and the absence of the mesoloph(-id) are other important dental characters distinguishing *Pseudoryzomys* from all oryzomyines.

Remarks

Pseudoryzomys is the semi-aquatic representative of the phyllotine rodents. Its adaptations for a palustrine and aquatic habitat compare with those of *Oryzomys palustris*. They fall short of those already attained by *Nectomys* among oryzomyines and *Holochilus*

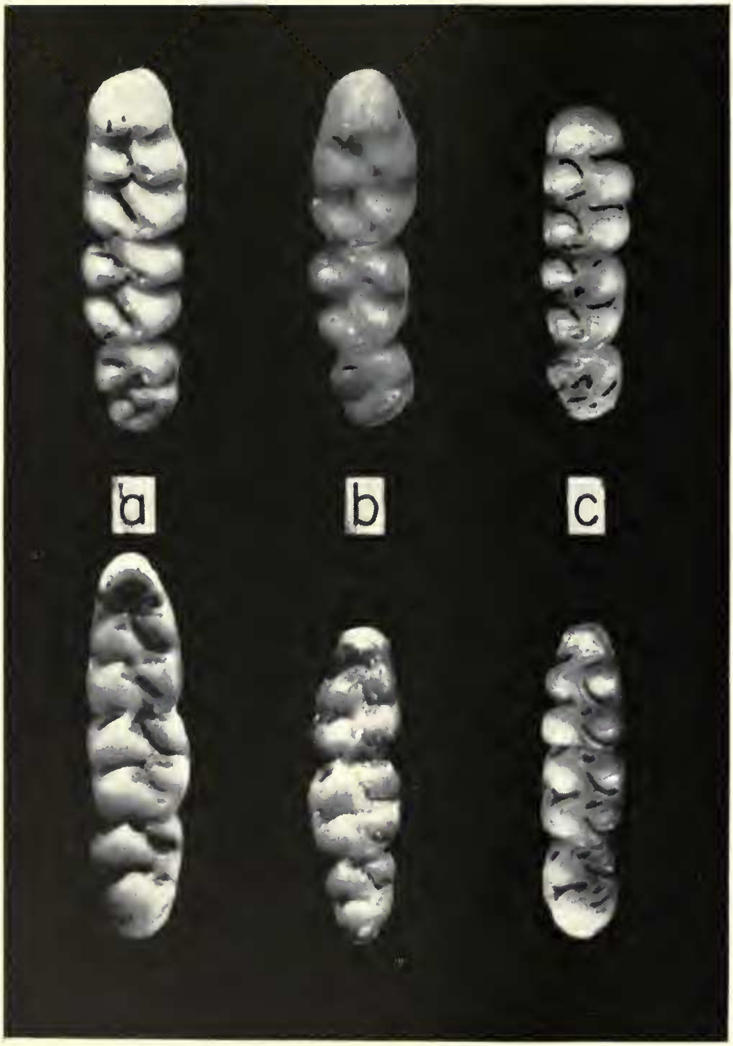


FIG. 56.—Upper and lower molars of *a*, *Pseudoryzomys wavrini; b*, *Calomys callosus; c*, *Oryzomys palustris.*

among sigmodonts. The phyllotine *Zygodontomys* is less modified for a palustrine habitat than *Pseudoryzomys*, and its direction of evolution is toward the vole-like rather than the natatorial type.

TABLE 10.—Measurements of *Pseudoryzomys wavrini* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
PARAGUAY							
Jesematathla[1]	106	106	25	16	28.8	15.5	4.8
Misión	120	120	26	17	30.3	16.2	5.0
ARGENTINA							
Tacaagle	105[2]	110[2]	29[2]	12[2]	—[3]	14.0	4.8

[1] Type.
[2] External measurements from dry skin.
[3] Condylo-incisive length 25.3 (in type, 26.6).

Pseudoryzomys wavrini Thomas

Oryzomys wavrini Thomas, 1921, Ann. Mag. Nat. Hist., (9), 7: 177. Ellerman, 1941, The families and genera of living rodents, 2: 341, 354.

Pseudoryzomys wavrini Hershkovitz, 1959, Proc. Biol. Soc. Washington, 72: 9—PARAGUAY: *Chaco Boreal* (Jesematathla; Misión); ARGENTINA: *Formosa* (Tacaagle, Río Porteño).

Type.—"Young adult male" skin and skull, British Museum (Natural History) no. 20.12.18.16; collected 15 August, 1920, by the Marquis de Wavrin.

Type locality.—Jesematathla, west of Concepción, Chaco Boreal, Paraguay; altitude, 100 meters above sea level.

Distribution (fig. 52).—Chaco Boreal of Paraguay and Chaco Central, Formosa in Argentina.

Characters.—Those of the genus.

Remarks.—In describing *wavrini* as an *Oryzomys* Thomas was misguided by a certain amount of convergence in a few superficial characters. The diagnostic cranial characters and similarities with such truly related forms as the sympatric *Calomys callosus* were overlooked, and the absence of the mesoloph(-id), the "cross-crochet" of Thomas, was brushed aside as a "mere abnormality." Ellerman (supra cit.) regarded *wavrini* as aberrant within the framework of the genus *Oryzomys*. He did note (p. 341), however, its resemblances to *Hesperomys* (=*Calomys*).

Nothing is known of the habits of *Pseudoryzomys wavrini*. The morphology indicates that *Pseudoryzomys* fills nearly the same ecological niche among phyllotines as *Nectomys* does among oryzomyines and *Holochilus* among sigmodonts.

The characterization of *Pseudoryzomys* is based primarily on a subadult male at hand from Misión Tacaagle, Río Porteño, Chaco Central, Argentina, collected 27 November, 1925, by Hans Krieg. The type of *Oryzomys wavrini*, with which comparison was made, is fully adult and in thick winter (August) pelage.

Measurements.—See Table 10 (p. 215).

Specimens Examined.—Total 3. PARAGUAY.—*Chaco Boreal:* Jesematathla, 1, the type (BM); Misión, 1 (BM). ARGENTINA —*Formosa:* Tacaagle, Río Porteño, 1 (CNHM).

Genus **Phyllotis** Waterhouse

Phyllotis Waterhouse, 1837, Proc. Zool. Soc. London, **1837**: 28—subgenus of *Mus;* included species, *darwini, xanthopygus, griseoflavus,* Thomas, 1884, Proc. Zool. Soc. London, **1884**: 449—subgenus of *Hesperomys; Mus darwini* Waterhouse, type by selection. Thomas, 1896, Proc. Zool. Soc. London, **1896**: 1020—full genus. Thomas, 1897, Ann. Mag. Nat. Hist., (6), **20**: 550—in text; generic rank. Thomas, 1916, op. cit., (8), **17**: 141—diagnosis. Osgood, 1947, Jour. Mammal., **28**: 165. Pearson, 1958, Univ. California Publ. Zool., **56**: 391—revision.

Auliscomys Osgood, 1915, Field Mus. Nat. Hist., Zool. Ser., **10**: 190—subgenus of *Phyllotis; Reithrodon pictus* Thomas, type. Thomas, 1926, Ann. Mag. Nat. Hist., (9), **17**: 317—genus. Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 210—subgenus of *Phyllotis.*

Graomys Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 141—genus; type, *Mus griseoflavus* Waterhouse. Osgood, 1916, Field Mus. Nat. Hist., Zool. Ser., **10**: 207—subgenus of *Phyllotis.* Thomas, 1919, Ann. Mag. Nat. Hist., (9), **3**: 495—genus. Osgood, 1947, Journ. Mammal., **28**: 170—subgenus of *Phyllotis.*

Paralomys Thomas, 1926, Ann. Mag. Nat. Hist., (9), **17**: 315—*Phyllotis gerbillus* Thomas, type. Osgood, 1947, Journ. Mammal., **28**: 171—subgenus of *Phyllotis.*

Loxodontomys Osgood, 1947, Journ. Mammal., **28**: 172—subgenus of *Phyllotis;* type, *Mus micropus* Waterhouse.

Hesperomys, Thomas (not Waterhouse), 1884, Proc. Zool. Soc. London, **1884**: 449—part, *Phyllotis* subgenus, only. Ellerman, 1941, The families and genera of living rodents, London, **2**: 446, 448—part, *Paralomys,* subgenus only.

Eligmodontia, Thomas (not Cuvier), 1898, Proc. Zool. Soc. London, **1898**: 210—part, *Phyllotis griseoflavus* only. Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9**: 132 and footnote—*domorum, cachinus* only.

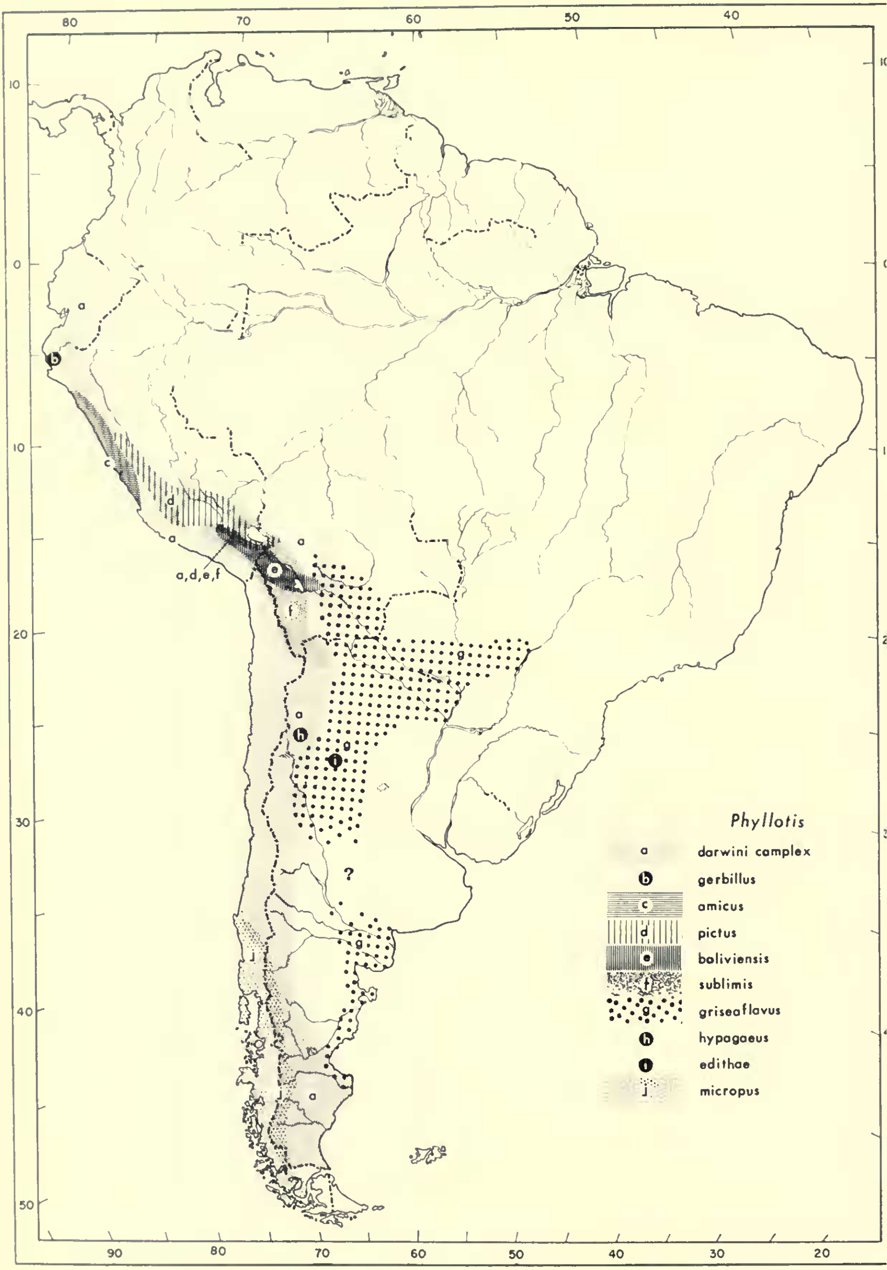
Euneomys, Thomas (not Coues), 1901, Ann. Mag. Nat. Hist., (7), **8**: 254—part, species *pictus* and *sublimis* only. Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 143—part, *Auliscomys* subgenus, only.

Type species.—Mus darwini Waterhouse (=*Phyllotis darwini* Waterhouse) by subsequent designation (Thomas, 1884, p. 449).

Included species.—Phyllotis darwini, osilae, andium, haggardi, micropus, gerbillus, boliviensis, sublimis, pictus, griseoflavus, edithae, amicus, hypogaeus.

Distribution
(Figures 52, 57)

From the Ecuadorian Andes at the equator south along the Andes and coast of Peru and Chile to the Straits of Magellan, west over the


80
70
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0
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90
80
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b
c
d
a
a,d,e,f
a
e
f
g
a
h
g
i
?
g
j
a
Phyllotis
a darwini complex
b gerbillus
c amicus
d pictus
e boliviensis
f sublimis
g griseaflavus
h hypogaeus
i edithae
j micropus

FIG. 57.—Distribution of the species of *Phyllotis*.

Bolivian Andes into the Paraguayan Chaco, and continuing southward through the Andes, Sierras Pampeanas, Chaco and Patagonian regions of Argentina; altitudinal range from sea level to over 5,500 meters above, or to limits of perpetual snow. The species of the *Phyllotis darwini* complex (*darwini, osilae, andium, haggardi*) range over most of the area occupied by the genus from tropical zone to temperate zone, in deserts and on humid mountain sides. In contrast, *Phyllotis gerbillus* is restricted to a few hundred square miles of desert about Piura in northwestern Peru. *P. micropus* is known only from the cold, humid cordilleras that form the boundary between southern Chile and Patagonia. The treeless, sandy and rocky highlands above 3400 meters in Peru, Bolivia, northern Chile, and northern Argentina are inhabited by *P. sublimis.* The range of *P. boliviensis* is the same, except that it does not extend into Argentina. *P. pictus* is a third highland form not known from Argentina and Chile, but its range extends farthest north in Peru. *Phyllotis griseoflavus* prefers the scrublands from sea level to nearly 3000 meters above, in Argentina, Paraguay and Bolivia. A similar species, *P. amicus,* occupies the semiarid scrublands of western Peru. Two species, *edithae* and *hypogaeus,* from Argentina, are of uncertain status and known only from the types. Both occur within the range of *Phyllotis griseoflavus griseoflavus* and it has been suggested (cf. p. 455) that they are identical with it.

Characters

External.—External form adapted for terrestrial and scansorial life; size variable, pelage long, fine; body elongate, tail shorter to longer than combined head and body length; ears large, length from notch shorter to longer than hindfoot length; postauricular patches sometimes present, rarely conspicuous; fifth hind toe (fig. 3), less claw, reaching distal end of first phalanx of fourth toe, the first hind toe at least to base of first phalanx of second toe. Underside of heel hairy, remainder of sole naked or, sometimes, with a sparse covering of short bristles; plantar pads naked, six in number, the middle three usually enlarged but not coalesced; mammae eight.

Cranial (figs. 58–60).—Dorsal contour of skull flat or slightly convex; supraorbital region broad or narrow with sides parallel, concave or divergent; fronto-parietal sutures crescentic in outline, not forming a right or oblique angle at midline, combined width on dorsal surface usually more than greatest width across fronto-maxillary sutures and more than alveolar length of molar row; interparietal well developed; palate broad, greatest width between inner borders of first molars more than length of $m^{\underline{1}}$; pitted posterolateral portion of palate little to moderately excavated; width of mesopterygoid fossa, measured at anterior base of pterygoid processes, approximately equal to greatest width of $m^{\underline{2}}$, always more than width of $m^{\underline{3}}$, but less than width of parapterygoid fossa measured at same plane; parapterygoid fossa shallow or moderately excavated.

Dental (figs. 59, 67–69).—Upper incisors variable in position, their anterior face grooved or smooth. Molar crowns low or moderately high; occlusal surface of unworn or moderately worn molar plane or terraced, outline of individual cusps, as seen on occlusal surface, usually subovate but often tending to triangulation or lamination; upper first molars with 4, sometimes 3 roots, lower with 3 or 4 roots; procingulum of first upper molar ovate, triangular or subcordate in outline, never completely divided into two conules; anteroloph of $m^{\underline{2}}$ reduced or well developed, of $m^{\underline{3}}$ reduced or absent; postcingulum of all upper molars obsolete or absent; first minor folds of $m^{\underline{2-3}}$ obsolete or absent; a vestigial mesoloph sometimes present; discrete internal folds absent; procingulum of $m_{\overline{1}}$ usually undivided; procingulum obsolete in $m_{\overline{2-3}}$; postcingulum of $m_{\overline{1}}$ present and normally well developed, of $m_{\overline{2}}$ present but may be obsolete in worn tooth, of $m_{\overline{3}}$ vestigial or absent; minor fold present at least in slightly worn $m_{\overline{2}}$, obsolete or absent in $m_{\overline{3}}$.

Comparisons

The genus *Phyllotis* is distinguished from genera of the *Calomys* section (*Calomys, Eligmodontia, Zygodontomys*) by molars terraced or planed, not crested (figs. 14, 49), procingulum of $m^{\underline{1}}$ uniconulate, mesostyle absent or extremely reduced; from *Calomys* and *Zygodontomys* by the long outer toes of hind foot; from *Zygodontomys* by finer pelage, narrower mesopterygoid fossa and more broadly expanded parapterygoid fossa; from *Eligmodontia* by generally larger size and absence of hairy cushion on sole of hind foot. Compared with other genera of the phyllotine section (figs. 3, 61–63, 69) the typical genus is distinguished from *Galenomys* primarily by the practically naked distal half of sole, flat or slightly convex dorsal contour of skull, and by greater width of mesopterygoid fossa relative to width of third upper molar; from *Chinchillula* and *Andinomys* by smaller size, broader palate relative to length of first upper molar, less hypsodont molars, and less triangulate cusps; from *Chinchillula* by absence of well-defined contrasting color pattern on upper parts;

from *Andinomys* by ordinary orientation of the upper incisors at median line; from *Pseudoryzomys* by smaller feet, longer outer digits, hairy heel and generally broader skull.

Similarities between South African *Mystromys* and New World *Phyllotis* noted by Ellerman (1941, pp. 444, 445) are common to many cricetines while differences in certain details of cranial and dental structure definitely separate *Mystromys* from all other genera. A skull of *Mystromys* (figs. 60, 64–66) compared with skulls of phyllotines reveals the following distinctive characters: Coronoid and condylar processes of mandible long, slender and subequal in length; exposed portion of lower incisor about one and one-half times length of lower molar row; parapterygoid fossa deep (but approximately equal in *Chinchillula*); external auditory meatus directed ventrally as well as laterally; sphenopalatine vacuities large but lateral wings of presphenoid fully ossified (thinly ossified and largely fenestrated in phyllotines); incisive foramina extremely narrow, parallel-sided and longer than in phyllotines; preorbital foramen sac-like, the lateral wall inflated (compressed, with slit-like opening in phyllotines); premaxillary extending anteriad to nasal and both elements lying posteriad to antero-vertical plane of incisors; interorbital region relatively narrower than in phyllotines; interparietal narrow anteroposteriorly, subtrapezoidal in outline with long base posteriad; median longitudinal occipital crest well developed and backward sloping (weakly defined or absent in phyllotines); molars (figs. 66, 67) crested (most nearly as in *Zygodontomys*), pattern greatly simplified, with pro- and post-cingula reduced, and without mesoloph(-id) or mesostyle(-id); third molar less than one-half size of second and with second primary fold rotated posteriorward (also see pp. 24, 107 for additional remarks on *Mystromys*).

Variation

The largest species, *Phyllotis griseoflavus*, is a fourth smaller than full-grown house rats of the genus *Rattus*. The smallest species, *P. gerbillus*, is the size of the house mouse, *Mus musculus*. The tail varies from nearly half again as long as head and body length in the scansorial *P. griseoflavus*, to as little as a third as long in the vole-like *sublimis*. In pilosity and color, the tail varies almost as much intraspecifically as intragenerically. The high Andean *P. sublimis* has moderate-sized ears, but it lives side by side with extremely large-eared *P. boliviensis*. Even greater contrast in size exists between the smallest-eared *P. gerbillus* of the desert coast of northern Peru and its geographic neighbor, *P. amicus*, with very large ears. The desert dwelling *P. gerbillus* is also the palest species, while the darkest, *P. micropus*, inhabits the cold, humid Patagonian Andes. The same correlation between color of animal and humidity of habitat obtains throughout the range of the genus.

The small, delicately formed skull of *P. gerbillus* differs grossly from the large, angular one of *boliviensis*. Nevertheless, there is complete intergradation in cranial characters between all species of the genus (figs. 58, 59). A narrow parallel-sided or constricted interorbital region characterizes the *P. darwini* group, *micropus*, *boliviensis*, *sublimis* and *pictus*. The broad, divergent-sided type of interorbital region is found in *gerbillus*, *amicus* and *griseoflavus*, where it is extreme. However, some individuals of the *P. darwini* group, notably *P. darwini wolffsohni* and *P. amicus*, approach each other so nearly in the shape of the interorbital region that distinction between the two types is not always obvious. The zygomata are little expanded, practically parallel-sided in *darwini*, *gerbillus*, *griseoflavus*, become well-bowed in *boliviensis*, *sublimis* and *pictus*, and generally triangular-shaped in *P. micropus*. The interparietal is well developed in the genus, but rather small in *P. sublimis*. Bullae are neither markedly small nor exceptionally large in any species. They are most inflated in *P. boliviensis*, somewhat less in *griseoflavus*, and least in the *P. darwini* complex and *P. sublimis*.

Dental characters are fully intergrading among the species of *Phyllotis* (figs. 59, 67, 68). All molar crown modifications are based on the simplified or tetralophodont pattern, but the mesoloph appears occasionally in all species as a slight projection or, usually, as a mere sinuosity of the connecting enamel ridge between protocone and hypocone. The incisors vary in angle of projection, from opisthodont in most species to generally orthodont in *pictus* and chiefly proodont in *boliviensis*. Grooves of the anterior surface of the incisors are always present, though weakly etched, in *P. pictus*, less constantly present and faintly indicated in *sublimis*, and obsolete in *boliviensis*. Molar rows vary from parallel-sided in most species to convergent posteriorly in *haggardi* and *amicus*, divergent posteriorly in *micropus*, and bowed in some individuals of *boliviensis*. Molar crowns are lowest in *gerbillus*, highest in the *darwini* complex, *micropus* and *boliviensis*. The crowns are terraced in *gerbillus* and *pictus*, planed in the others, except in juvenals of *boliviensis*, *sublimis* and *amicus*. The horizontal outline of the cusps varies from ovate to triangulate whether in different species or within the same species. The enamel pattern of the second molar may be 8-shaped, modified S-shaped, or some intermediate design. The procingulum of second upper molar is present in adults of most species, weakly developed in *P. sublimis*, and considerably reduced in the *P. darwini* complex.

Taxonomy

All generic synonyms were based, originally, on single species. *Paralomys* Thomas and *Loxodontomys* Osgood were frankly proposed for a species each of *Phyllotis*. *Graomys* Thomas also proves to be monotypic, though it was first believed to include four "species." *Auliscomys* Osgood was set up on the basis of a comparison of its genotype, *P. pictus*, with *Phyllotis darwini*. Two other species, *P. sublimis* and *P. boliviensis*, were also referred to *Auliscomys*, but Osgood's definition of the genus excludes them. Relationships between each of the genotypes as well as the remaining species (*edithae* and *hypogaeus* not seen and excepted) are about the same, though not in the same order. As simple species of the genus *Phyllotis*, the status of each *vis-a-vis* the others remains exactly the same. Subgeneric names in this case are superfluous complications.

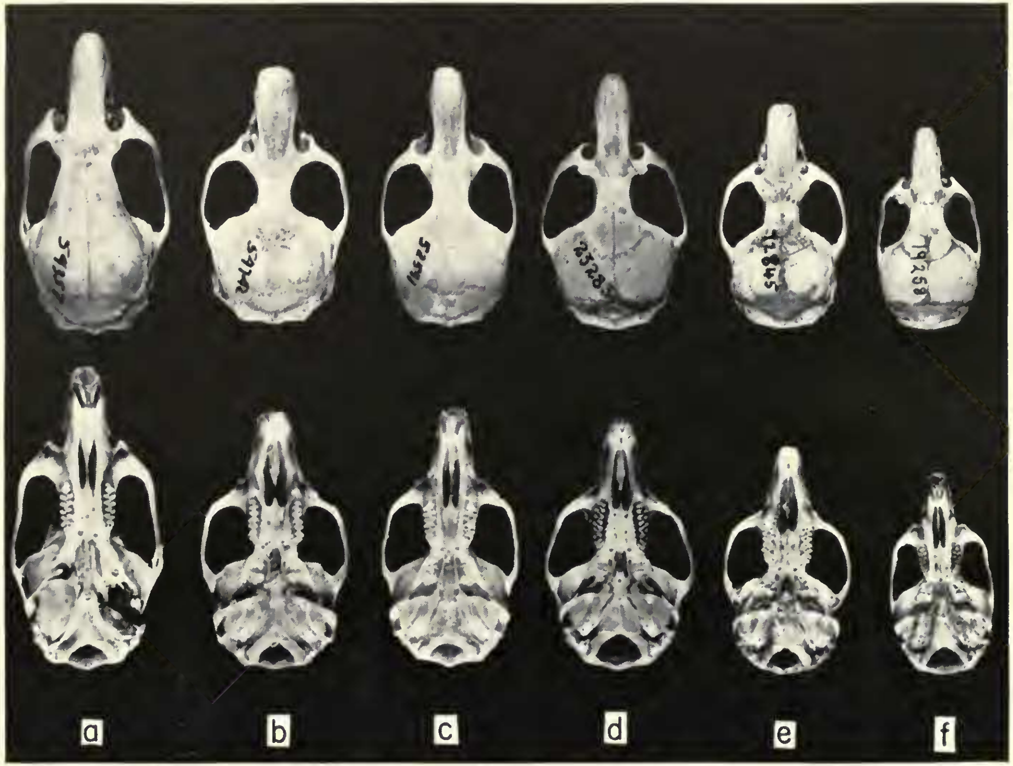


FIG. 58.—Species of *Phyllotis*. Dorsal and palatal aspects of skulls of *a*, *P. griseoflavus*; *b*, *P. pictus*; *c*, *P. darwini*; *d*, *P. micropus*; *e*, *P. sublimis*; *f*, *P. amicus*. (Slightly more than natural size.)

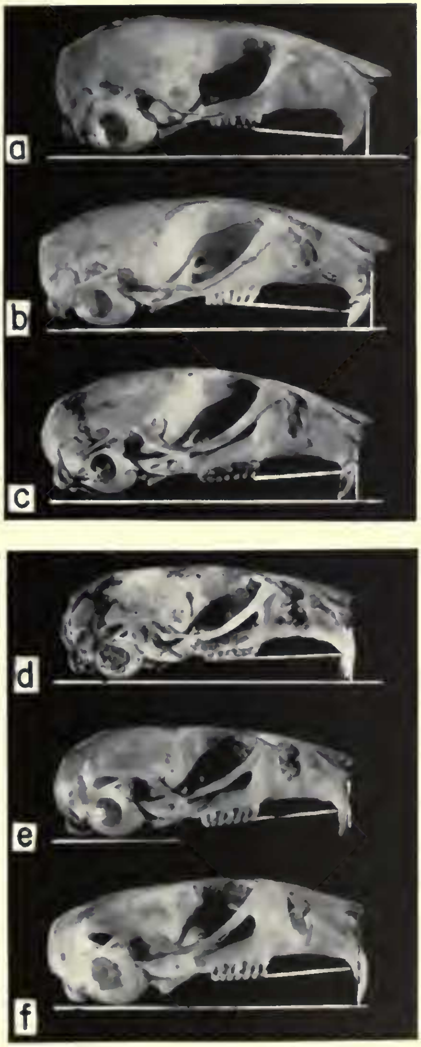


FIG. 59. Species of *Phyllotis*. Side view of skulls of *a*, *P. griseoflavus*; *b*, *P. darwini*; *c*, *P. micropus*; *d*, *P. sublimis*; *e*, *P. pictus*; *f*, *P. boliviensis*. Vertical-incisive, molar and basal-incisive planes shown by white line (cf. pp. 107–108).

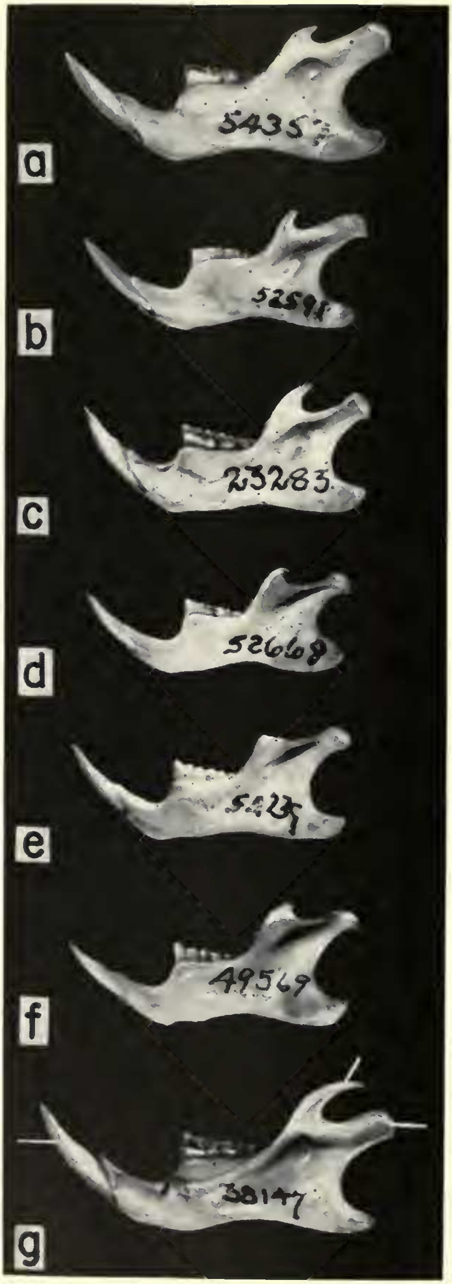

a
b
c
23283
d
e
f
49569
g
38147

FIG. 60.—Species of *Phyllotis* and *Mystromys*. Mandibles of *a*, *P. griseoflavus*; *b*, *P. darwini*; *c*, *P. micropus*; *d*, *P. sublimis*; *e*, *P. pictus*; *f*, *P. boliviensis*; *g*, *Mystromys albicaudatus*.

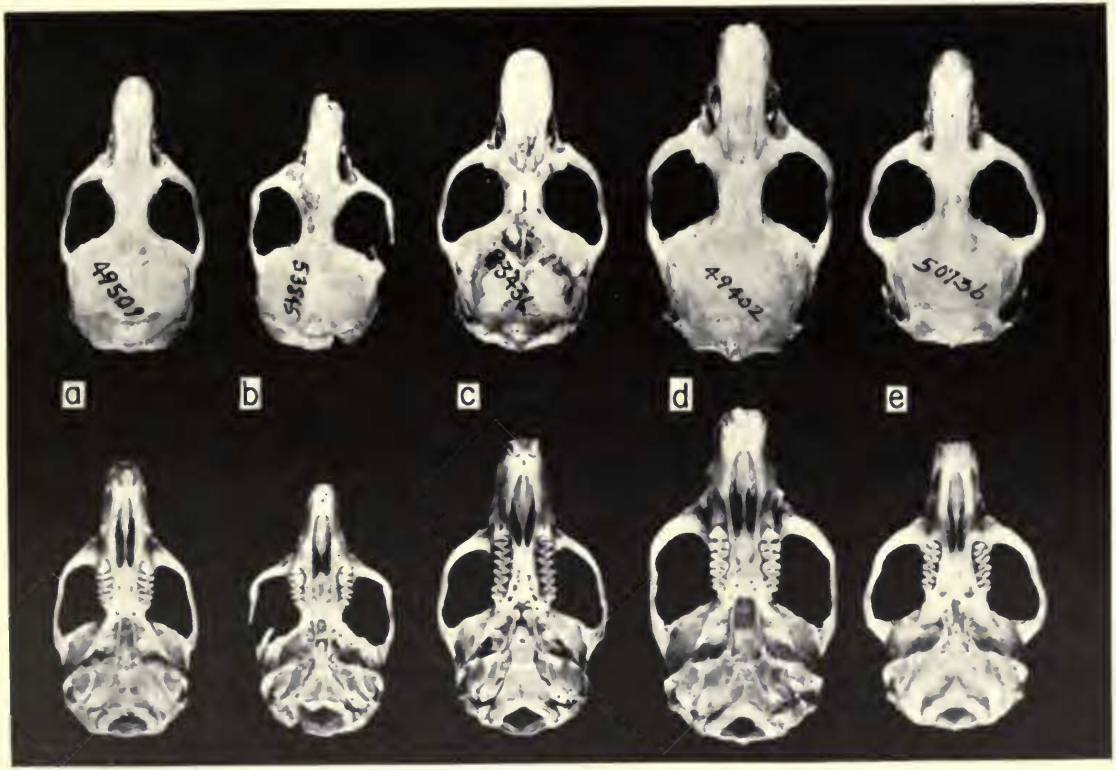

a
b
c
d
e
49501
53545
49402
50136

FIG. 61. Dorsal and ventral aspects of skulls of *a*, *Phyllotis darwini*; *b*, *Galenomys garleppi* (with nasal tips missing); *c*, *Andinomys edax*; *d*, *Chinchillula sahamae*; *e*, *Euneomys chinchilloides*. (Slightly more than natural size.)

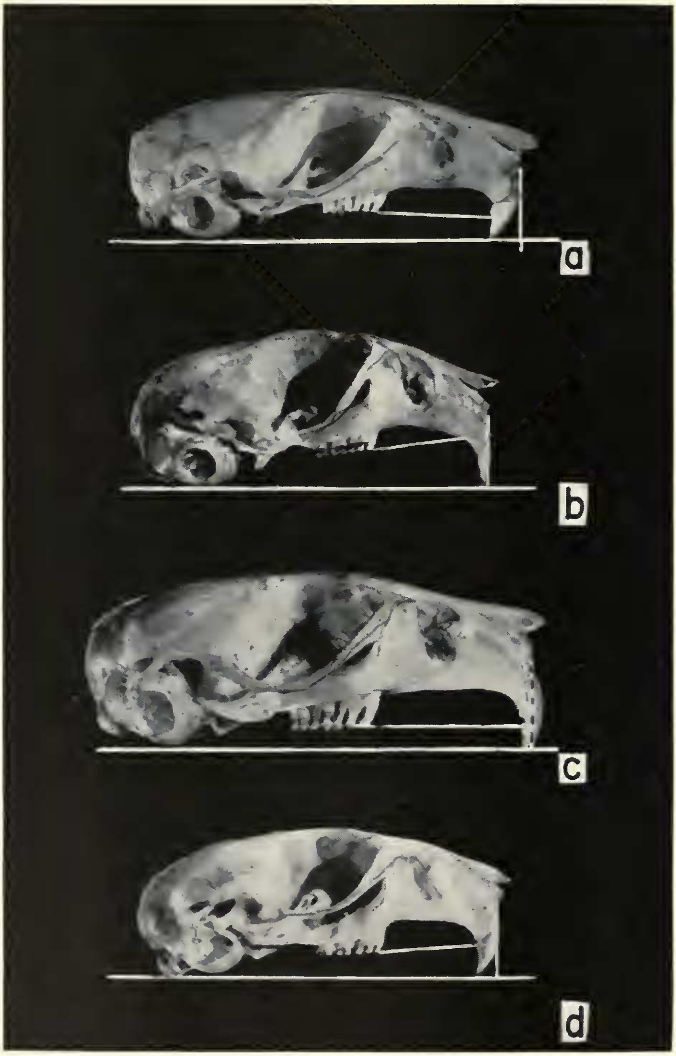


FIG. 62.—Side view of skulls of *a, Phyllotis darwini; b, Galenomys garleppi; c, Chinchillula sahamae; d, Euneomys chinchilloides.* Vertical-incisive, molar and basal-incisive planes shown by white lines. (About × 1½.)

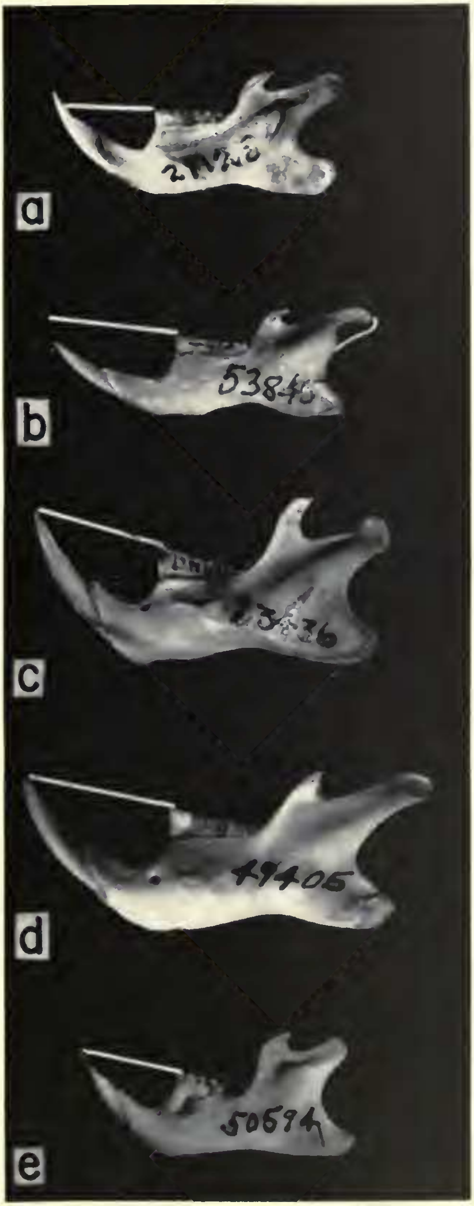

a
b
53840
c
d
49405
e
50594

FIG. 63. — Mandibles of *a*, *Phyllotis darwini*; *b*, *Galenomys garleppi*; *c*, *Andinomys edax*; *d*, *Chinchillula sahamae*; *e*, *Euneomys chinchilloides*. Relationship of incisor tips to molar plane shown by white line (cf. p. 108).

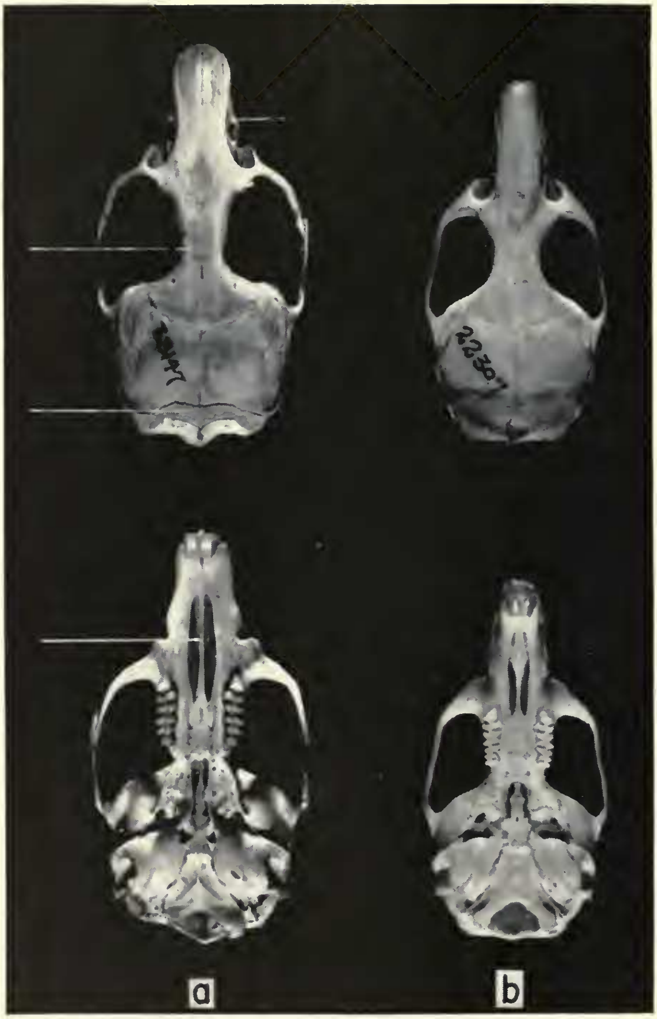


FIG. 64.—Dorsal and ventral aspects of skull of *a*, *Mystromys albicaudatus*; *b*, *Phyllotis darwini*. See comparisons in text, p. 221. (About × 1½.)

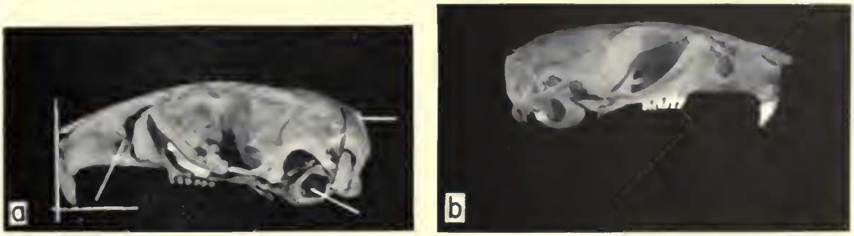


FIG. 65.—Side view of *a*, *Mystromys albicaudatus*; *b*, *Phyllotis darwini*. See comparisons in text, p. 221. (Slightly more than natural size.)

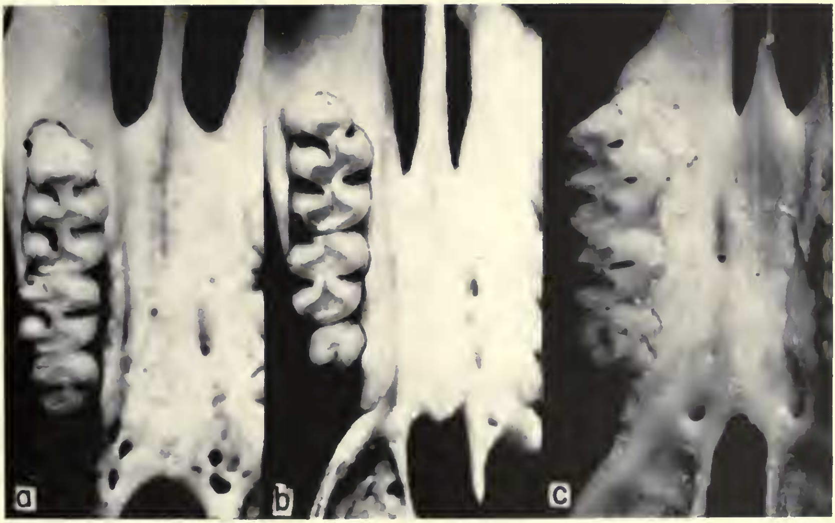


FIG. 66.—Palate and right upper molars of *a*, *Zygodontomys brevicauda*; *b*, *Mystromys albicaudatus*; *c*, *Phyllotis darwini*. See comparisons in text, p. 221.

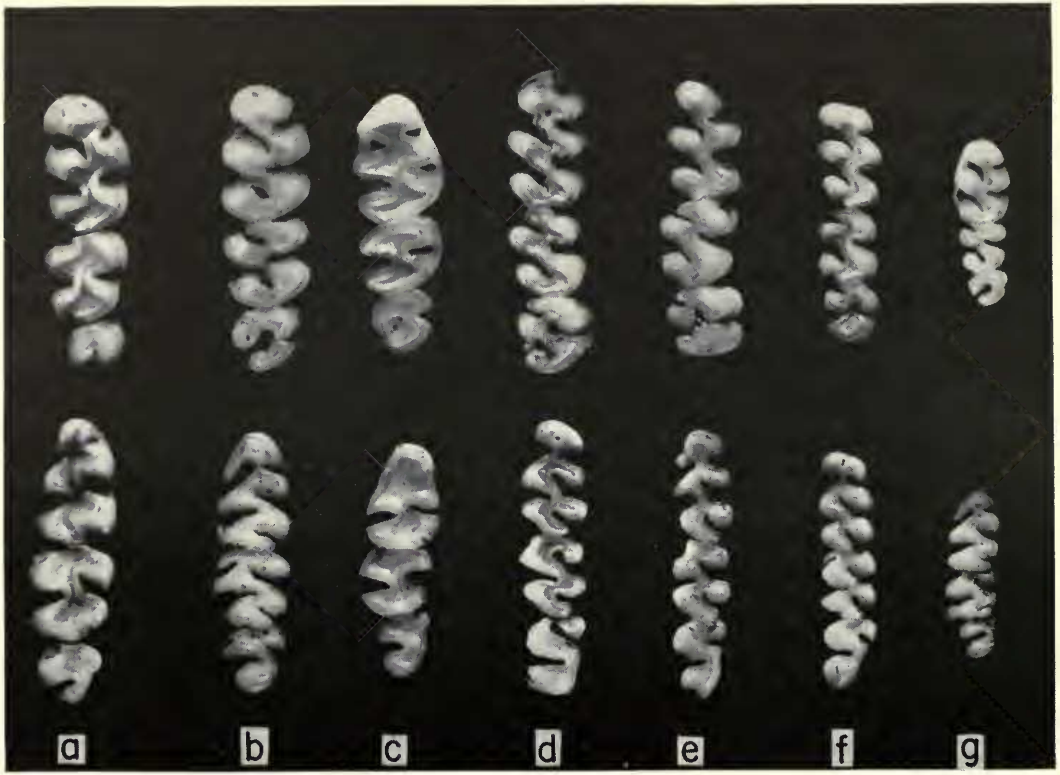


FIG. 67.—*Mystromys* and *Phyllotis.* Right upper and left lower molars of *a*, *Mystromys albicaudatus;* *b*, *Phyllotis griseoflavus;* *c*, *P. darwini;* *d*, *P. micropus;* *e*, *P. pictus;* *f*, *P. sublimis;* *g*, *P. amicus.*

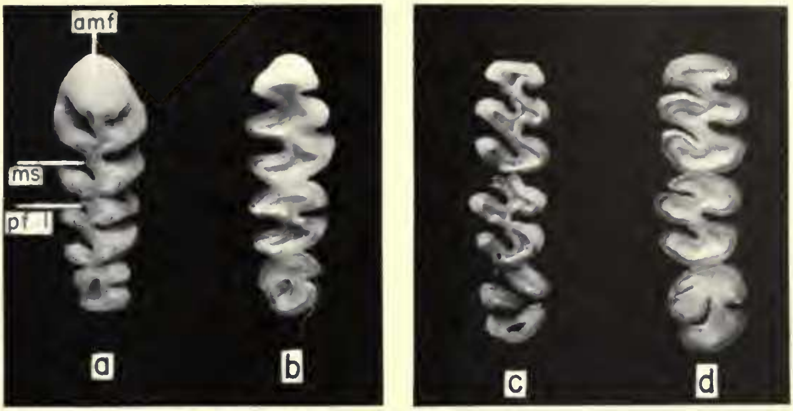
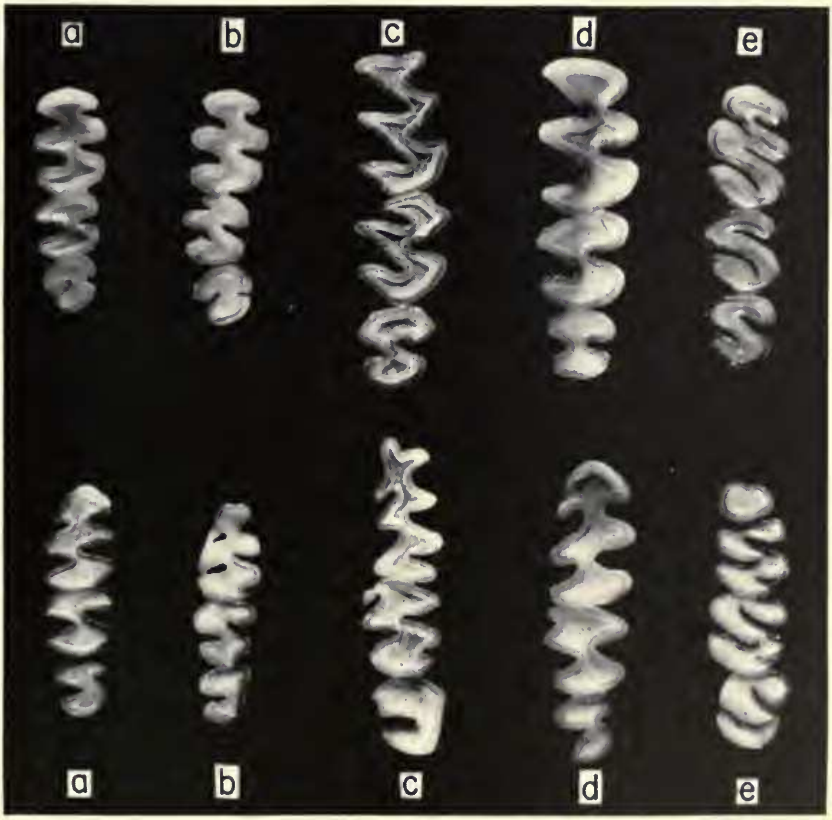

amf
ms
pf l
a
b
c
d

FIG. 68.—Right upper molars, unworn and worn of *a*, *b*, *Phyllotis darwini; c*, *d*, *P. micropus.*


a
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e
a
b
c
d
e

FIG. 69.— Right upper and left lower molars of *a*, *Phyllotis darwini; b*, *Galenomys garleppi; c*, *Andinomys edax; d*, *Chinchillula sahamae; e*, *Euneomys chinchilloides.*

Phyllotis darwini Complex

Distribution

(Figures 57, 70)

Savannas, scrublands and deserts from the Ecuadorian Andes south through the Andes and along the Pacific coast to the Straits of Magellan and to the Atlantic in the Patagonian region.

Definition

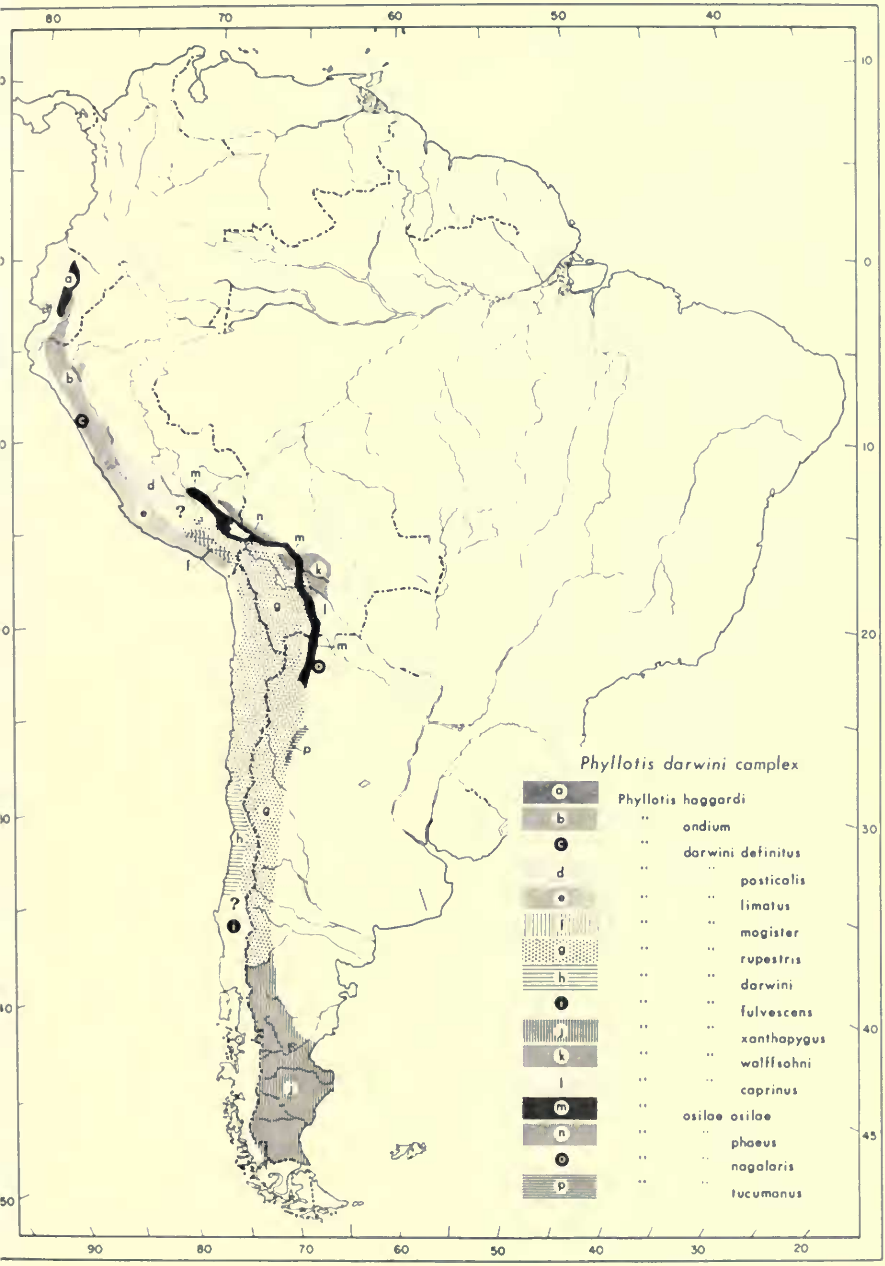
The *Phyllotis darwini* complex consists of the usual complement of broadly defined clinal subspecies, a pair of sympatric subspecies, and a group of ill-defined species or near species which are not certainly recognizable as taxons in allopatry but are not known to interbreed in sympatry.

The geographic relationship of the members of the complex is discussed elsewhere under the heading Sympatry and Allopatry (p. 31).

Characters

External.—Size moderate to nearly as large as *P. griseoflavus;* tail from approximately one-third less to two-fifths more than combined head and body length, sharply bicolor or slightly paler beneath than above, thinly to well haired but never markedly bushy, tip more or less pencilled; hind feet normal, soles naked except at heel, plantar tubercles well developed; ears moderate to large in size, length, from notch, rarely, if ever, as long as hind foot with claw; small pale postauricular patches often present. Upper parts of body buffy or ochraceous to dark brown, more or less mixed with black; head and sides of body with less black; ochraceous lateral line present or absent; underparts from sharply defined whitish to gray or from plumbeous washed with buff to brown and hardly or not at all defined from sides; base of hairs always dark; a pectoral streak or midventral line often present.

Cranial.—Interorbital region generally narrow, the sides concave, parallel or posterior half slightly to moderately divergent; borders square or slightly pinched upward, sometimes beaded or provided with narrow ledges; zygomata usually parallel-sided or convergent anteriorly, rarely well expanded, their greatest breadth less than distance between posterior tips of nasals and anterior


Phyllotis darwini complex
a Phyllotis haggardi
b " andium
c " darwini definitus
d " " posticalis
e " " limatus
f " " magister
g " " rupestris
h " " darwini
i " " fulvescens
j " " xanthopygus
k " " wolffsohni
l " " caprinus
m " osilae osilae
n " " phaeus
o " " nogalaris
p " " tucumanus
80
70
60
50
40
10
0
10
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30
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45
50
90
80
70
60
50
40
30
20

FIG. 70.—Distribution of the species and subspecies of the *Phyllotis darwini* complex.

border of supraoccipital; anterior border of infraorbital plate plane or slightly concave, the upper corner rounded, square, or pointed, never produced as a conspicuous spinous process; incisive foramina well opened; posterior border of palate square, or rounded and with or without a median spinous process; posterolateral palatal pits variable in size and position relative to anterior border of mesopterygoid fossa; bullae moderately inflated, their anteroposterior length, less tubes, approximately equal to or less than alveolar length of molar row; outer side of mandible with slightly projecting capsule for encasing base of incisor.

Dental.—Upper incisor ungrooved, opisthodont (fig. 19, A)[1] but combined width of cutting edges less than alveolar length of $m^{\underline{1}}$; molar rows parallel-sided or slightly convergent posteriorly; upper and lower first molars 4-rooted; molars hypsodont, crowns of upper plane, cusps ovate or subtriangular in outline; crowns of unworn lower molars slightly terraced; procingulum of $m^{\underline{2}}$ usually reduced, the first primary fold shallow and well defined in juvenal, often persistent in adult; moderately worn $m^{\underline{2}}$ with 8-shaped or S-shaped enamel pattern; a vestigial mesoloph sometimes present in $m^{\underline{1-2}}$; $m_{\overline{2}}$ with first minor and primary folds present in unworn, present or absent in worn condition.

Comparisons

Because of the community of their characters and the parallelisms in their individual and local variations, all members of the *Phyllotis darwini* complex are best compared as a unit with other species of the genus. Small, pale, long-tailed members of the group resemble large, similarly colored representatives of *Phyllotis amicus;* and small, pale, short-tailed individuals are superficially like *P. boliviensis.* Large, dark, short-tailed examples could be confused with *P. micropus* and large, pale, long-tailed group members resemble *P. griseoflavus.* Externally, the *P. darwini* complex is distinguished from *P. amicus* by larger size, tail generally shorter relative to head and body length, ears proportionately smaller and not as long as hind foot including claw; from *P. micropus* by tail relatively longer, hairier, pencilled, more distinctly bicolor, and pelage of body glossy and adpressed; from *P. griseoflavus* by underparts grayer, less sharply defined, with hairs of throat and neck slaty basally, tail usually shorter, less hairy basally, ears shorter; from *P. boliviensis* by over-all larger size and usually longer tail, preauricular patches absent, postauricular patches absent or inconspicuous.

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[1] Pearson (1958, pp. 413 ff.) describes the upper incisors of *Phyllotis darwini* as orthodont.

Dentally, members of the *darwini* complex, excepting *P. darwini wolffsohni*, differ from all congeners by the greater reduction of procingulum of m^{2-3} and postcingulum of m_{2-3}, with corresponding first primary folds and minor folds of worn teeth reduced or obsolete (fig. 67); these folds of the procingula are nearly always well developed in *P. darwini wolffsohni* (fig. 85, *d–f*). The comparatively long, narrow skull, slightly expanded zygomata, usually parallel- or concave-sided interorbital region, and moderately sized tympanic bullae (figs. 58–60) are cranial characters that singly or in combinations serve to distinguish members of the *darwini* complex from the species with which comparisons have been made. Such members of the *darwini* complex as *P. darwini wolffsohni* and *P. d. caprinus* (fig. 83) with more or less beaded and divergent-sided interorbital regions are distinguished by their narrower interorbital width as compared with *P. griseoflavus* and *P. amicus* with similarly shaped skulls.

EXPLANATION OF FIGURE 71

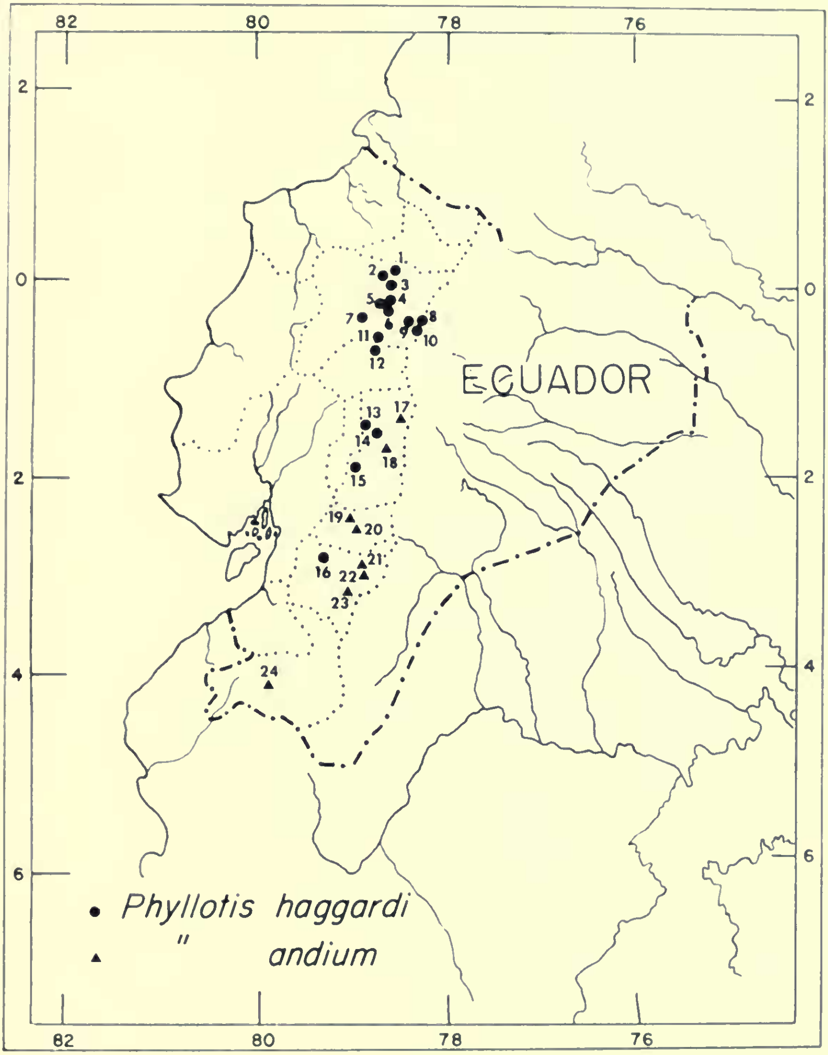
Phyllotis in Ecuador: collecting localities and collectors.
Type localities in **boldface**.

Phyllotis haggardi (1–16)

1. Mojanda (Mount), Pichincha.—Natives per L. Söderström at 8000–13,000 feet.
2. Perucho, Pichincha.—Natives per L. Söderström.
2. Puéllaro, between Perucho and Guaillabamba, Pichincha.—Natives per L. Söderström at 7500 feet.
3. Guaillabamba, Pichincha. —Natives per L. Söderström at 8000–9000 feet.
4. Puembo, Pichincha (2542 meters).—Native per L. Söderström at 8000 feet.
5. **Pichincha (Mount), Pichincha.**—Type locality of *haggardi;* F. Mena at 3800 meters; M. Olalla between 3000 and 4000 meters; natives per L. Söderström between 3000 and 4000 meters.
5. Garzón (Hacienda), southern foot of Mount Pichincha, Pichincha.—S. N. Rhoads at 12,000 feet.
6. Quito, Pichincha (2817 meters).—Natives per L. Söderström.
6. Jirón, Pichincha.—Natives per L. Söderström at 9400 feet.
7. Saloya, Pichincha.—F. Mena per Leopoldo Gomez at "1100 meters."
7. "Galaya, Cotopaxi."=Saloya, Pichincha.
8. Papallacta, Napo-Pastaza (3156 meters).—Native per L. Söderström.
9. Guamaní, Pichincha (3400 meters).—Record ex Pearson (1958, p. 443) at 11,000 feet.
10. Antisana (Mount), Pichincha.—W. Richardson at 12,000 feet; G. H. H. Tate at 13,500–15,000 feet; Clark McIntyre at 3500 meters; natives per L. Söderström at 12,000 feet.
11. Corazón (Mount), Pichincha.—Natives per L. Söderström.
12. Illiniza (Mount), Cotapaxi.—Native per L. Söderström.
13. Chimborazo (Mount), Chimborazo.—A. Mena at 4000–4200 meters.
14. Urbina, Chimborazo (3700 meters).—G. H. H. Tate.
15. **Pallatanga, Chimborazo** (1550 meters).—Type locality of *elegantulus;* C. Buckley.
16. **Contrayerbas, Azuay.**—Type locality of *fuscus;* G. H. H. Tate at 11,000 feet.

Phyllotis andium (17–24)

17. Baños, Tungurahua.—Record ex Pearson (1958, p. 441) at 5800 feet.
18. Punín, Chimborazo.—About 10 kilometers south of Ríobamba; G. H. H. Tate at 9000 feet.
18. Ríobamba, Chimborazo.—Record ex Pearson (1958, p. 441) at 9900 feet.
19. Pauichi (Paujchi), Chimborazo or Cañar.—Tate, Wickenheiser. "Half day by pack mule from Huigra on the Cañar trail."
20. **Cañar, Cañar.**—Type locality of *andium;* P. O. Simons at 2600 meters.
21. Cuenca, Azuay (2° 53′ S., 78° 59′ W.).—Record ex Pearson (1958, p. 441) at 7200 feet.
21. Guishapa, Azuay (2° 59′ S., 78° 57′ W.).—Record ex Pearson (1958, p. 441) at 6600 feet.
22. Sigsig, Azuay.—Record ex Pearson (1958, p. 441) at 8500 feet.
23. Yunguilla Valley, Azuay.—H. Cuestas at "1500 meters."
24. **Guachanamá, Loja.**—Type locality of *fruticicolus;* H. E. Anthony at 9050 feet.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ECUADOR
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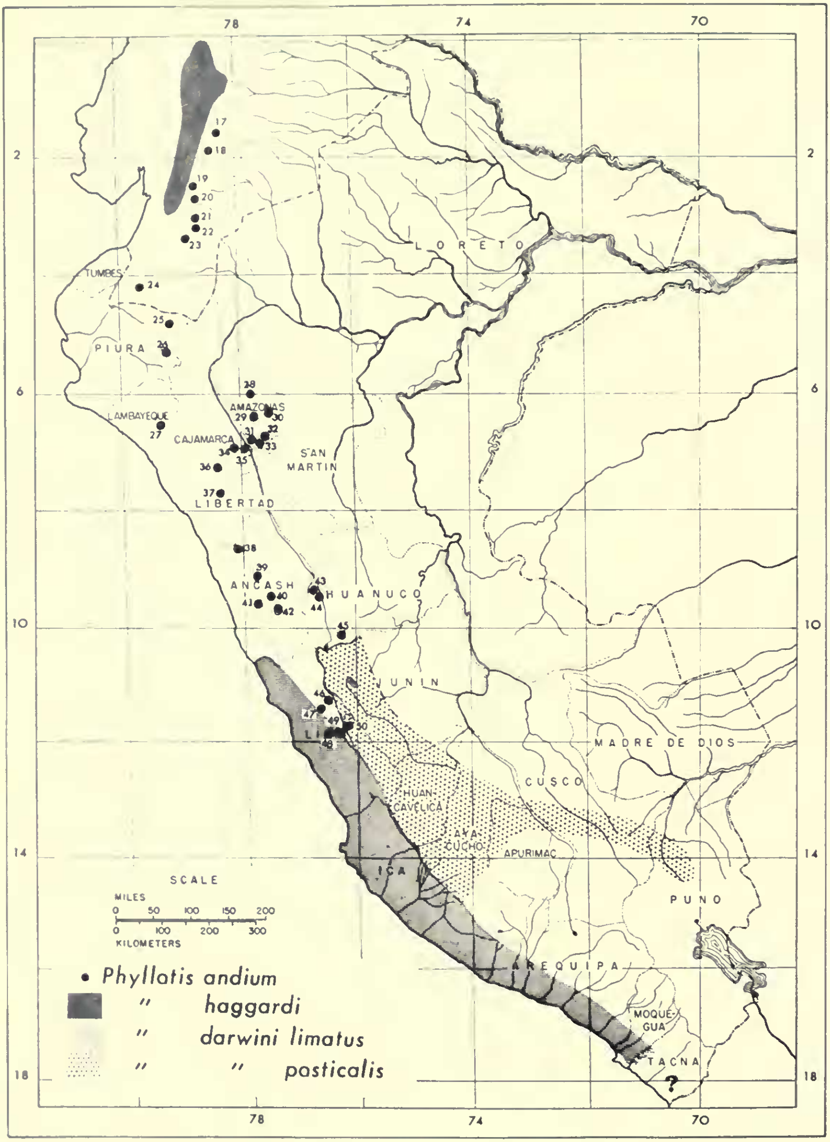
● Phyllotis haggardi
▲ " andium

Fig. 71. Collecting localities of *Phyllotis haggardi* and *P. andium* in Ecuador. See opposite page for explanation.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LORETO
TUMBES
PIURA
LAMBAYEQUE
AMAZONAS
CAJAMARCA
SAN MARTIN
LIBERTAD
ANCASH
HUANUCO
JUNIN
LIMA
MADRE DE DIOS
CUSCO
HUANCAVELICA
AYACUCHO
APURIMAC
ICA
PUNO
AREQUIPA
MOQUEGUA
TACNA
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SCALE
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0 100 200 300
KILOMETERS
● Phyllotis andium
" haggardi
" darwini limatus
" " posticalis

FIG. 72.—Collecting localities of *Phyllotis andium*. Shaded areas show approximate ranges of *P. haggardi* and some subspecies of *P. darwini* in Peru. See opposite page for explanation.

EXPLANATION OF FIGURE 72

Phyllotis andium: collecting localities and collectors.
Type localities in **boldface**.

ECUADOR

17-24. See explanation of figure 71 (p. 238) for names of localities.

PERU

25. Ayavaca, Piura (2750 meters).—C. Kalinowski.
26. Huancabamba, Piura (1960 meters).—C. Kalinowski.
27. Chongoyape, Lambayeque (240 meters).—C. Kalinowski.
27. Cabache (=Cayache?), Lambayeque (460 meters).—About 12 kilometers northeast of Chongoyape; C. Kalinowski.
28. Goncha, Amazonas.—North of Chachapoyas; R. W. Hendee at 8000-9500 feet.
29. Condechaca, Amazonas (1550 meters).—About 15 kilometers south of Chachapoyas; R. W. Hendee at 7000 feet.
29. Chachapoyas, Amazonas (2398 meters).—W. H. Osgood and M. P. Anderson; H. Watkins at 7500 feet.
30. Molinopamba, Amazonas (2350 meters).—R. W. Hendee.
31. **TAMBO CARRIZAL,** Amazonas.—Type locality of *tamborum*; W. H. Osgood and M. P. Anderson at 5000 feet.
32. San Pedro, Amazonas.—About 12 kilometers northeast of Leimabamba; H. Watkins between 8600-9400 feet.
32. Leimabamba, Amazonas (2500 meters).—R. W. Hendee.
33. **UTCUBAMBA (Río), 51 miles above Chachapoyas, Amazonas.**—Type locality of *stenops;* W. H. Osgood and M. P. Anderson at 8000 feet; R. W. Hendee.
34. Celendín, Cajamarca (2500 meters).—R. W. Hendee.
35. Limón (Hacienda), Cajamarca.—W. H. Osgood at 3000 feet.
36. Cajamarca, Cajamarca (2750 meters).—W. H. Osgood and M. P. Anderson; R. W. Hendee.
37. Llagueda (Hacienda), Libertad.—W. H. Osgood at 6000 feet.
37. Otuzco (mountains near), Libertad.—W. H. Osgood and M. P. Anderson at 10,000 feet.
38. Macate, Ancash.—M. P. Anderson at 9000-10,000 feet.
39. Yungay, Ancash (2335 meters).—C. Kalinowski.
40. Huaras, Ancash (3091 meters).—C. Kalinowski at 3050 meters.
40. Quilcayhuanca (Quebrada), Ancash.—Northeast of Huaras; C. Kalinowski at 4000 meters.
41. Pira, Ancash.—R. W. Hendee at 13,000 feet.
42. Catac (Hacienda), Ticapampa, Ancash.—C. Kalinowski at 3500 meters.
43. Llata, Huánuco.—R. W. Hendee at 11,000 feet.
44. Cullcui, Huánuco.—J. T. Zimmer at 10,400 feet.
45. Ambo, Huánuco (2152 meters).—E. Heller.
46. Huarés, Lima.—O. P. Pearson at 11,500-12,000 feet.
47. Canta, Lima.—O. P. Pearson at 8800 feet.
48. Surco, Lima (2050 meters).—M. Puestas.
48. Santa Eulalia, Lima.—O. P. Pearson at 3500 feet.
49. Matucana, Lima (2336 meters).—J. T. Zimmer.

Explanation of Figure 72 (*continued*)

49. San Bartolomé Station, Lima.—About 12 kilometers southwest of Matucana; O. P. Pearson at 5200 feet.
49. San Mateo, Lima.—About 12 kilometers northwest of Matucana; O. P. Pearson at 9500 feet.
49. Zarate, Lima.—About 5 kilometers southwest of Matucana; O. P. Pearson at 9000 feet.
50. Casapalca, Lima.—O. P. Pearson at 13,200–14,000 feet.
50. Villavista, Lima.—About 7 kilometers southwest of Casapalca; O. P. Pearson at 12,200 feet.

EXPLANATION OF FIGURE 73

Phyllotis darwini in Peru: collecting localities and collectors.

Type localities in **boldface**.

Phyllotis darwini definitus (1)

1. **Macate, Ancash.**—M. P. Anderson at 9000 feet.

Phyllotis darwini limatus (2–14)

2. Huacho, Lima (30 meters).—J. J. von Tschudi.
3. Lima, Lima, 156 meters.—Capital of Peru; no collecting records.
4. Naña, Lima.—O. P. Pearson at 2200 feet.
5. Chosica, Lima.—P. O. Simons; C. C. Sanborn at 3000 feet; O. P. Pearson at 3500 feet.
5. Rimac Valley.—O. P. Pearson at 4400 feet.
6. Santa Eulalia, Lima.—J. T. Zimmer; O. P. Pearson at 4000 feet.
7. Huinco, Lima.
8. San Bartolomé Station, Lima.—O. P. Pearson at 5200 feet.
8. Verruga Canyon.—Dr. Tyzzer.
9. Surco, Lima.—O. P. Pearson at 6000 feet.
9. Oscollo, Lima.—M. Puestas.
10. La Palma, Lima.
11. San Jacinto, Ica, Ica.—C. C. Sanborn.
12. Atico, Arequipa.—C. B. Koford at 50 feet.
13. Tambo, Arequipa.
14. Chucarapí, Arequipa.—C. B. Koford at 300 feet.

Phyllotis darwini posticalis (15–42)

15. Huariaca, Pasco.—R. W. Hendee at 9000 feet.
16. Carhuamayo, Junín.—C. C. Sanborn at 14,500 feet.
17. Junín, Junín (4133 meters).—M. P. Anderson.
18. **Oroya = La Oroya, Junín** (3720 meters).—Type locality of *abrocodon;* R. W. Hendee; M. P. Anderson.
19. **Galera, Junín.**—Type locality of *posticalis;* P. O. Simons at 4800 meters.
20. Casapalca, Lima.—O. P. Pearson at 13,200–14,000 feet.
21. Mantaro (Río), Huancavelica.—O. P. Pearson at 8500 feet.
22. Piso (Hacienda), Locroja, Huancavelica.—C. Kalinowski at approximately 3100 meters.
23. Mayoc, Huancavelica.—C. Kalinowski at approximately 2500 meters.

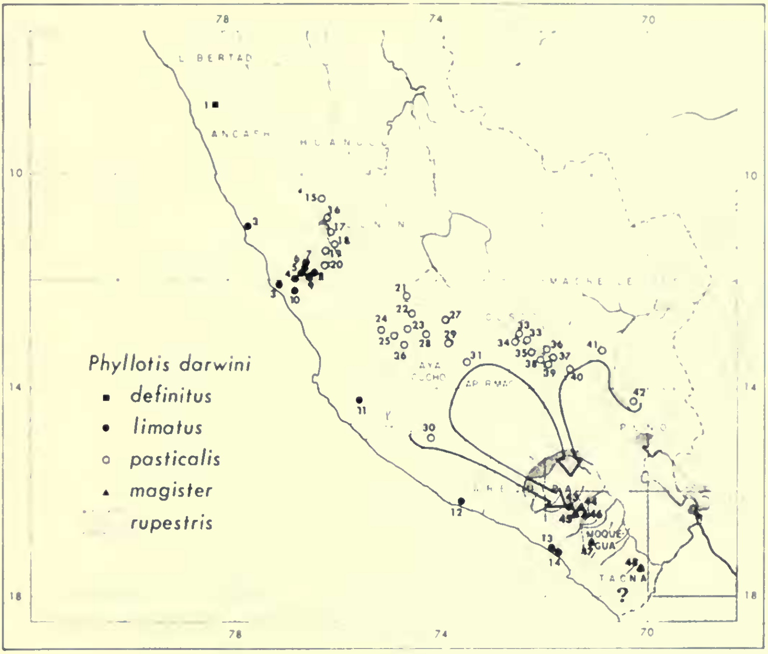
Phyllotis darwini
■ definitus
● limatus
○ posticalis
▲ magister
rupestris
LIBERTAD
ANCASH
HUANUCO
AYACUCHO
APURIMAC
MADRE DE DIOS
PUNO
MOQUEGUA
TACNA
78
74
70
10
14
18
?

FIG. 73.—Collecting localities of the subspecies of *Phyllotis darwini* in southern Peru. The approximate range of *P. d. rupestris* is shaded. *P. d. rupestris* and *P. d. magister* are independent offshoots of *P. d. posticalis* that have become sympatric.

Explanation of Figure 73 (*continued*)

24. Huancavelica, Huancavelica (3716 meters).—C. Kalinowski at 3680 meters.
25. Lircay, Huancavelica (2714 meters).—C. Kalinowski at 3310 meters.
26. San Jenaro, Santa Inéz, Huancavelica.—C. Kalinowski at 4760 meters.
27. Polanco, Tambo, Ayacucho.—C. Kalinowski.
28. Ayacucho, Ayacucho.—O. P. Pearson at 9500 feet.
29. Puente Pajonal, Ocros, Ayacucho.—C. Kalinowski at 1900 meters.
30. Puquio, Ayacucho.—O. P. Pearson at 14,600 feet (35 kilometers ENE of Puquio), 13,500 feet (15 kilometers ENE); C. B. Koford at 14,500 feet.
31. Palmira (Hacienda), Andahuaylas, Apurimac.—C. Kalinowski at 2200 meters.
32. Occobamba Valley, Cusco.—E. Heller at 9100 feet.
32. Tocopoqueu, Cusco.—E. Heller at 9100 feet.
33. Ollantaytambo, Cusco.—E. Heller at Occobamba Pass, 15 kilometers north of Ollantaytambo, 9300 feet.
34. Macchu Picchu, Cusco (2331 meters).—E. Heller at 6000–13,000 feet.
35. Chospioc, Cusco.—E. Heller at 10,000 feet.
35. Huarocondo, Cusco.—E. Heller at 10,850 feet.
36. Urco (Hacienda), Calca, Cusco (3000 meters).—E. Heller; J. M. Schmidt.
36. Paullo Grande, Calca, Cusco.—C. Kalinowski at 2900 meters.

Explanation of Figure 73 (*continued*)

37. Ampay, Pisac, Cusco.—C. Kalinowski at 3500 meters.
38. Puquiura, Cusco.—E. Heller at 9500 feet.
39. Sacsahuaman, Cusco, Cusco.—A pre-Columbian fortress overlooking Cusco; C. C. Sanborn at 11,500 feet.
39. Cusco, Cusco (3496 meters).—C. C. Sanborn.
39. Fundo Perayoc, Cusco.—I. Ceballos.
40. Ocongate, Cusco (3465 meters).—C. Kalinowski.
41. Ccolini, Marcapata, Cusco.—C. Kalinowski at 3900 meters.
42. Limbani, Puno.—C. B. Koford at 13,000 and 15,000 feet.

Phyllotis darwini magister (43–48, all sympatric with *P. d. rupestris*).

43. Yura, Arequipa.—J. M. Schmidt at 8000 feet.
44. Misti (Mount), Arequipa (5860 meters).—P. O. Simons at 2500 meters.
45. **Arequipa, Arequipa.**—P. O. Simons at 2300 meters; H. E. Anthony and G. Ottley.
46. Tingo, Arequipa.—Southeastern outskirts of Arequipa; G. H. H. Tate at 7500 feet.
46. Chihuata, Arequipa.—M. and C. B. Koford at 10,000 feet.
47. Torata (Río), Moquegua.—15 kilometers northeast of Torata; A. K. and O. P. Pearson at 11,200 feet.
48. Tarata, Tacna.—A. K. and O. P. Pearson at 11,000–12,800 feet.

EXPLANATION OF FIGURE 74

Phyllotis darwini: locality records and collectors of subspecies of *P. darwini* in southern Peru, Bolivia, northern Chile and northern Argentina.

Phyllotis darwini rupestris (1–93)

PERU

1. Ongoro, Valle de Mages, Arequipa.—C. C. Sanborn.
2. San Ignacio, Arequipa.—O. P. Pearson at 13,000 feet.
2. Cailloma, Arequipa (4330 meters).—P. O. Simons; C. C. Sanborn and J. M. Schmidt at 14,500 feet.
3. Sibayo, Arequipa.—O. P. Pearson at 11,500 feet.
4. Pulpera, Arequipa.
5. Huaylarco, Arequipa.—A. K. Pearson at 15,300 feet; C. B. Koford at 15,000 feet.
6. Imata, Arequipa.—M. and C. B. Koford at 14,500 feet.
7. Sumbay, Arequipa.—C. C. Sanborn and J. M. Schmidt at 13,500 feet.
8. Yura, Arequipa.—J. M. Schmidt at 8000 feet.
9. Arequipa, Arequipa (2335 meters).—P. O. Simons; H. E. Anthony and G. Ottley; A. K. and O. P. Pearson at 8800 feet.
10. Balneario de Jesús, Arequipa.—C. C. Sanborn at 8900 feet.
11. Misti, Arequipa.—P. O. Simons.
12. Salinas, Arequipa.—C. C. Sanborn at 14,000 feet; C. B. Koford at 14,200 feet.
13. Asillo, Puno.—C. C. Sanborn; C. B. Koford at 13,000 feet.
13. Osila, Puno.—See Asillo.
14. Arapa, Puno.—M. Koford at 12,600 feet.
15. Juliaca, Puno (3825 meters).—J. M. Schmidt at 12,500 feet; M. Koford.
16. Umayo, Puno.—C. B. Koford at 12,700 feet.

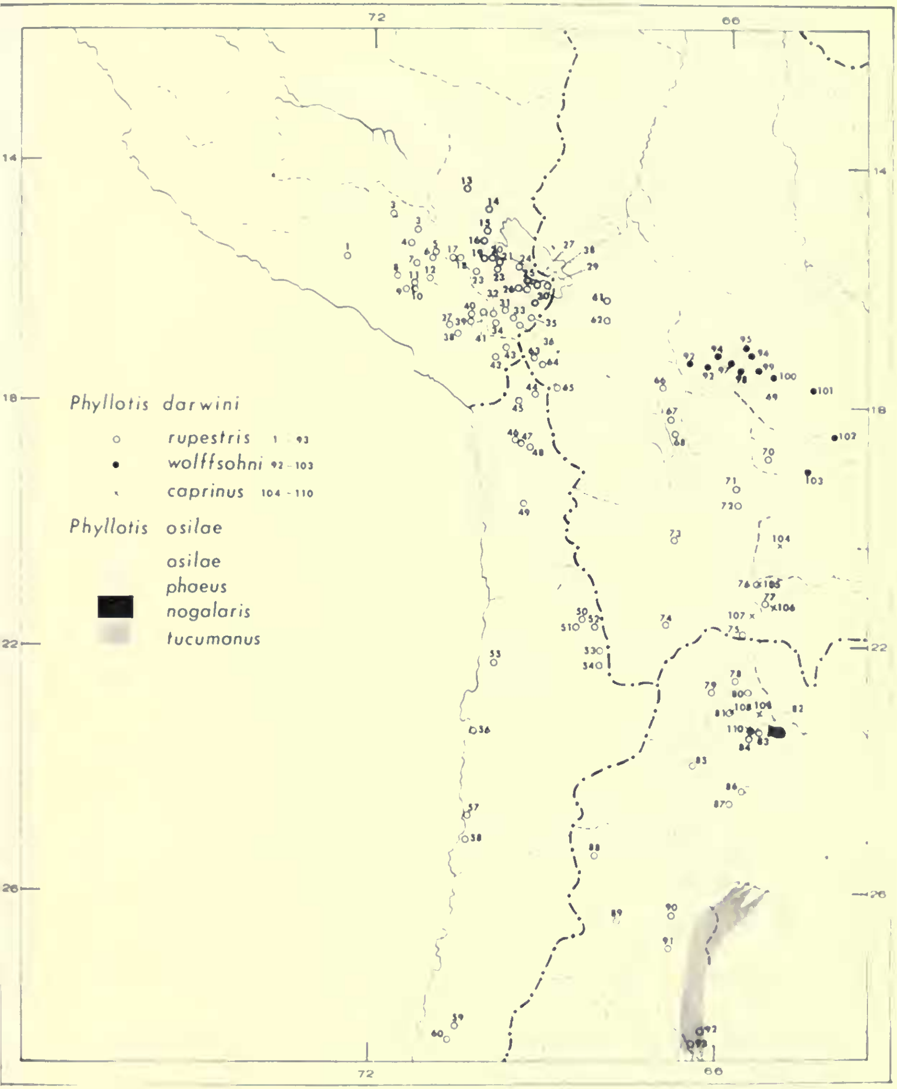
72
68
14
18
22
26
Phyllotis darwini
○ rupestris 1 – 93
● wolffsohni 92 – 103
× caprinus 104 – 110
Phyllotis osilae
osilae
phoeus
nogalaris
tucumanus

Fig. 74.—Collecting localities of the subspecies of *Phyllotis darwini* in southern Peru, Bolivia, and northern Chile and Argentina. Shaded areas show the approximate range of each of the subspecies of sympatric *Phyllotis osilae*.

Explanation of Figure 74 (*continued*)

17. 82 kilometers west of Puno.—A. K. and O. P. Pearson at 14,000 feet.
18. Tincopalca, Puno.—C. B. Koford at 13,500 feet.
19. Occomani, Puno.—E. Zúñiga.
20. Puno, Puno (3822 meters).—M. R. Portugal; A. K. and O. P. Pearson and C. B. Koford at 13,000 feet.
21. Chucuito, Puno.—C. C. Sanborn.
22. San Antonio de Esquilache, Puno.—C. C. Sanborn at 15,000 feet.
23. Collacachi, Puno.—C. C. Sanborn at 12,000 feet.
24. Ilave, Puno.—O. P. Pearson at 12,600 feet.
25. Juli, Puno.—O. P. Pearson at 12,500–12,700 feet.
26. Pairumani, Puno (4062 meters).—O. P. Pearson at 12,800 feet; C. B. Koford at 13,000 feet.
27. Sorapa, Puno.—H. E. Anthony and G. Ottley.
28. Pomata, Puno.—O. P. Pearson at 13,500 feet.
29. Yunguyo, Puno.—C. C. Sanborn at 13,000 feet.
30. Huacullani, Puno.—C. C. Sanborn.
31. Santa Rosa de Juli, Puno.—O. P. Pearson at 14,000 and 15,000 feet.
32. Caccachara, Puno.—O. P. Pearson at 15,200 and 16,000 feet.
33. Mazocruz, Puno.—C. B. Koford at 14,300 feet.
34. Río Santa Rosa, Puno.—A. K. and O. P. Pearson at 14,400 feet; C. B. Koford.
35. Pisacoma, Puno.—C. C. Sanborn at 13,200 feet.
36. Pampa de Ancomarca, Puno.—A. K. and O. P. Pearson at 14,200 feet.
37. Torata, Moquegua.—A. K. Pearson at 9400 feet, 10 kilometers NE.; A. K. and O. P. Pearson at 11,200 feet, 15 kilometers NE.
38. Tala, Moquegua.—A. K. Pearson at 13,700 feet.
39. Volcán Tutupaca, Moquegua.
40. Lago Suche, Moquegua.—O. P. Pearson at 14,500 feet; A. K. Pearson at 14,600 feet, 5 kilometers E.
41. Lago Viscacha, Moquegua.—A. K. Pearson at 14,900 feet.
42. Tarata, Tacna.—A. K. and O. P. Pearson at 11,500 feet, 2 kilometers N.; at 12,200 feet, 3 kilometers N.; at 12,800 feet, 4 kilometers N.; A. K. Pearson at 13,200 feet, 4.5 kilometers N.; A. K. and O. P. Pearson at 13,500 feet, 5 kilometers N.; 14,600 feet, 20 kilometers NE.; O. P. Pearson at 15,200 feet, 25 kilometers NE.; C. B. Koford, 13,000 feet, 8 miles NE.
43. Nevado Livine, Tacna.

CHILE

44. **Parinacota, Tarapacá.**—Type locality of *osgoodi* Mann and *chilensis* Mann; G. Mann.
45. Putre, Tarapacá (4560 meters).—G. Mann; C. C. Sanborn at 11,600 feet.
46. Codpa, Tarapacá (2109 meters).—G. Mann.
46. **Timar, Parinacota, Tarapacá.**—Type locality of *chilensis* Mann.
47. Esquiña, Tarapacá.—G. Mann.
48. Caritaya, Tarapacá.—C. B. Koford at 12,000 feet.
49. Tarapacá, Tarapacá (1350 meters).—G. Mann.
50. Ojos de San Pedro, Antofagasta.—M. and C. B. Koford at 12,500 feet.
51. **San Pedro, Antofagasta** (2436 meters).—F. Philippi; type locality of *glirinus* Philippi, *lanatus* Philippi.

Explanation of Figure 74 (*continued*)

52. San Pedro, 20 miles E., Antofagasta (3223 meters).—C. C. Sanborn.
53. Toconce, Antofagasta.—M. and C. B. Koford at 14,000 feet.
54. Tatio Geysers, Antofagasta.—C. B. Koford at 14,000 feet.
55. **Cobija, Antofagasta** ("high mountains" of).—Type locality of *rupestris* Gervais; M. Gaudichaud (voyage *La Bonite*).
56. **Antofagasta, Antofagasta.**—Type locality of *capito* Philippi.
57. Paposa, Antofagasta.
58. **Hueso Parado, Taltal,** Antofagasta (sea level).—F. Philippi.
58. Muelle de Piedra, east of Taltal.—Not located; see Hueso Parado.
59. Vallenar, Atacama.
60. Domeyko, Atacama (778 meters).—C. C. Sanborn.

BOLIVIA

61. La Paz, La Paz.—Specimens from 20 miles south; O. P. Pearson at 13,000 feet.
62. Cosmini, La Paz.—14,400 feet.
63. Estación Pérez, La Paz.—F. Steinbach at 3913 meters.
63. General Pérez, La Paz.—See Estación Pérez.
64. Esperanza, Pacajes, La Paz.—F. Steinbach at 4200 meters.
65. Sahama (Mt.), Oruro.—F. Steinbach at 4350 meters.
66. Oruro, Oruro (3700 meters).—P. O. Simons.
67. Oruro, 40 miles S., Oruro.—O. P. Pearson at 12,000 feet.
68. Chianta, Oruro.—At 12,000 feet.
69. Tin Tin, Cochabamba.—J. Steinbach.
70. Sucre, Chuquisaca.
71. Potosí, Potosí (4020 meters).
72. Potosí, 20 miles S., Potosí.—O. P. Pearson at 12,300 feet.
73. **Uyuni, Potosí.**—Type locality of *arenarius* Thomas; O. P. Pearson at 12,600 feet; P. O. Simons at 3670 meters.
74. Lipez (=San Antonio de Lipez), Potosí (4510 meters).—E. Budín at 4500 meters.
75. Villazón, Potosí.—O. P. Pearson at 11,500 feet, 5 miles N. and 25 miles N.
76. Camataquí, Tarijá.—O. P. Pearson at 11,500 feet, 25 miles SSE.
77. Sama, Tarija.—E. Budín at 4000 meters.

ARGENTINA

78. Abrapampa, Jujuy (3475 meters).—E. Budín at 3500 meters.
79. Cerro Casabindo, Jujuy.—E. Budín at 4000 meters.
80. Tres Cruces, Jujuy (3632 meters).—E. Budín at 4000 meters.
81. Sierra de Zenta, Jujuy.—E. Budín at 4500 meters.
82. Tilcara, Jujuy.—O. P. Pearson at 8500 feet.
83. Alfarcito, Jujuy.—E. Budín.
84. La Laguna, Sierra de Zenta, Jujuy.—J. Yepes at 4500 meters.
84. Cerro de Lagunita, Jujuy.—E. Budín at 4500 meters.
85. San Antonio de los Cobres, Salta.—E. Budín at 3700 meters.
85. San Antonio, Los Andes.—See San Antonio de los Cobres.
86. G. M. Sola, Salta.—E. Budín at 2500 meters.
87. Incamayo, Salta.
88. Salar de Antofalla, Los Andes (=Catamarca).
89. Pasto Ventura, Catamarca.

Explanation of Figure 74 (*continued*)

90. **Laguna Blanca, Catamarca.**—Type locality of *oreigenus* Cabrera; E. Budín at 3200 meters; J. Mogensen at 3200 meters; Weiser.
91. Lago Helado, Catamarca.
92. **Otro Cerro, Catamarca.**—Type locality of *ricardulus* Thomas; E. Budín at 3000 meters.
93. Chumbicha, Catamarca.—E. Budín at 500 meters.

Phyllotis darwini wolffsohni (92–103)

BOLIVIA

92. Tapacari, Cochabamba.—O. P. Pearson at 9000 feet, 15 miles E.
93. Parotani, Cochabamba.—L. E. Miller and H. S. Boyle at 8800 feet.
94. Cochabamba, Cochabamba (2464 meters).—J. Steinbach at 2700 meters.
94. Taquiña, Cochabamba.—Suburb of Cochabamba; J. and F. B. Steinbach at 2700–2750 meters.
95. Cuchicancha, Cochabamba.—L. E. Miller and H. S. Boyle at 11,000 feet.
96. Tiraque, Cochabamba.—F. B. Steinbach at 3200 meters.
97. Punata, Cochabamba.—O. P. Pearson at 10,000 feet, 8 miles NE., and 10,500 feet, 10 miles NE.
98. Arani, Cochabamba.—At 9000 feet.
99. Pocona, Cochabamba.—F. B. Steinbach at 2700 meters.
100. Totora, Cochabamba.—At 8500 feet.
101. Comarapa, Santa Cruz.—O. P. Pearson at 7500 feet.
102. Guadelupe, Santa Cruz.—Marzan and Machiavello.
103. Tomina, Chuquisaca.—R. M. Gilmore at 2200 meters.

Phyllotis darwini caprinus (104–110)

BOLIVIA

104. Camargo, Chuquisaca.—O. P. Pearson at 8500 feet.
105. Camataquí, Tarija.—O. P. Pearson at 8500 feet, 20 miles SSE.
106. Tarija, Tarija.—O. P. Pearson at 6700 feet.
107. Yuruma, Potosí.—E. Budín at 2200 meters; O. P. Pearson at 10,500 feet.

ARGENTINA

108. Sierra de Zenta, Jujuy.—E. Budín at 4500 meters.
109. Humahuaca, Jujuy.—At 7700 feet.
110. Tilcara, Jujuy.—L. E. Miller and H. S. Boyle at 8000 feet; O. P. Pearson at 8000 feet.
110. Maimará, Jujuy.—E. Budín at 2230 meters.

EXPLANATION OF FIGURE 75

Phyllotis darwini: locality records and collectors of subspecies of *P. darwini* in Chile and Argentina (continued from fig. 74).

Phyllotis darwini rupestris (1–29)

ARGENTINA

1. Lago Helado, Catamarca.—See no. 91, fig. 74.
2. **Otro Cerro, Catamarca.**—Type locality of *ricardulus* Thomas; E. Budín at 3000 meters.
3. Chumbicha, Catamarca (415 meters).—E. Budín at 500 meters.

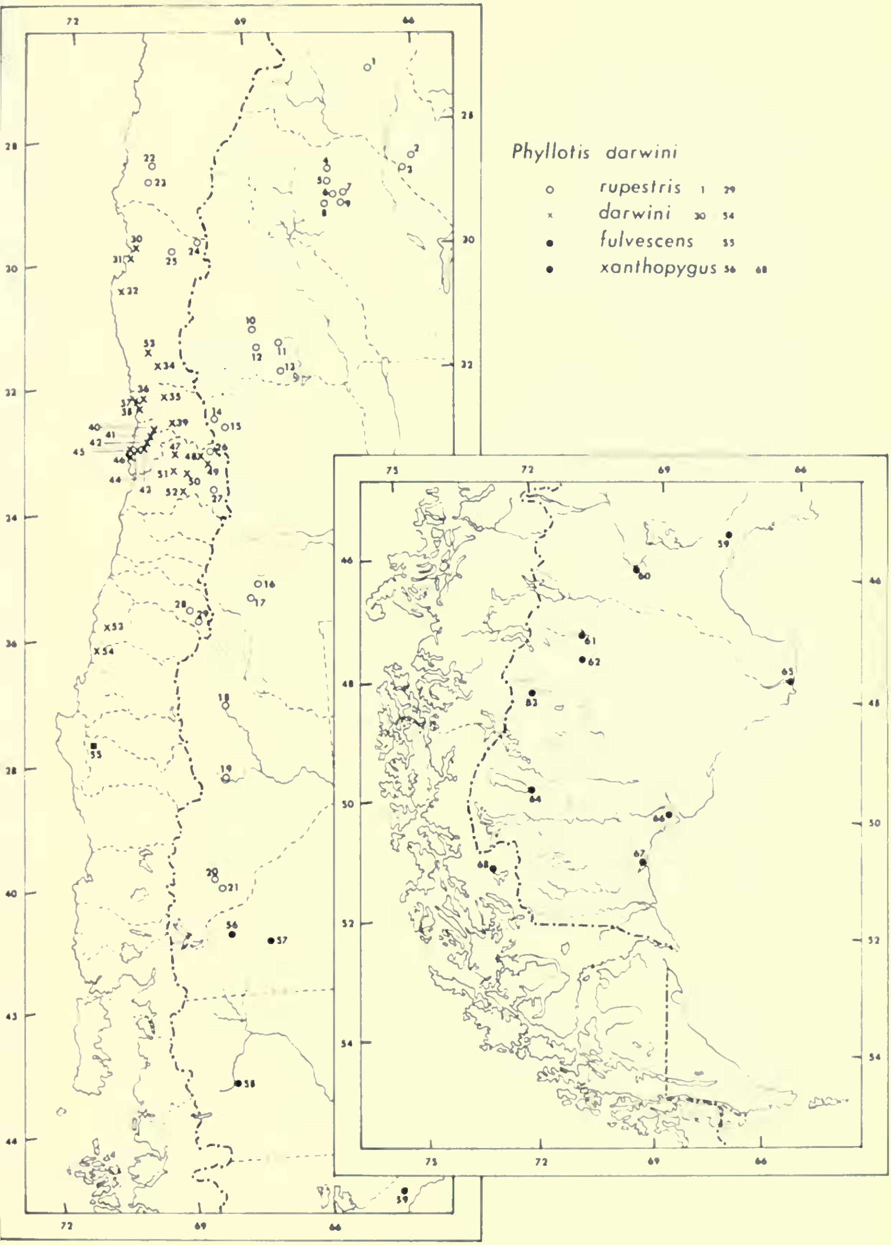
Phyllotis darwini
○ rupestris 1 29
× darwini 30 54
● fulvescens 55
● xanthopygus 56 68
72
69
66
75
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FIG. 75.—Collecting localities of the subspecies of *Phyllotis darwini* in Argentina and Chile.

Explanation of Figure 75 (*continued*)

4. La Invernada, Cadena Famatina, La Rioja.—E. Budín at 3800 meters.
5. Potrerillos, La Rioja (2500 meters).—E. Budín.
6. Chilecito, La Rioja.—J. Yepes at 1000 meters.
7. Puesto Viejo, La Rioja.—J. Yepes at 2500 meters.
8. Las Piriquitas, La Rioja.—J. Yepes.
9. San Antonio, La Rioja.—J. Yepes at 2700 meters.
10. Sierra de Tontal, San Juán.—E. Budín.
11. Angaco Sud, San Juán.
12. Los Sombreros, San Juán.—E. Budín at 2700 meters.
13. Pedernal, San Juán.
14. Puente del Inca, Mendoza (2720 meters).—E. Budín; H. E. Anthony and G. Ottley.
15. **Punta Vacas, Mendoza** (2385 meters).—Type locality of *vaccarum* Thomas; P. O. Simons; E. Budín at 2300–2500 meters.
15. Las Vacas, Mendoza.—See Punta Vacas.
16. Cañada Colorada, Mendoza (440 meters).—J. Yepes.
17. Malarguë, Mendoza (1450 meters).—J. Yepes.
18. Chos Malal, Neuquén (1395 meters).—E. Budín.
19. Las Lajas, Neuquén (710 meters).—E. Budín.
20. Quilquihue, Neuquén.—E. Budín.
21. Collon Cura, Neuquén.—E. Budín.

CHILE

22. Vallenar, Atacama.
23. Domeyko, Atacama (778 meters).—C. C. Sanborn.
24. Baños del Toro, Coquimbo (3258 meters).—C. C. Sanborn at 10,600 feet.
25. Paihuano [Paiguano], Coquimbo.—C. C. Sanborn at 3300 feet.
26. Río Blanco, Santiago.—R. Barros V., at 1540 meters.
27. **Bocatoma, Santiago** (1800 meters).—Type locality of *wolffhuegeli* Mann; G. Mann.
27. Lo Valdés, Santiago.—W. and G. Mann.
28. Río Maule, 14 km. above Curillinque, Talca.—C. C. Sanborn.
29. Arroyo del Valle, Talca.—C. C. Sanborn.

Phyllotis darwini darwini (30–54)

CHILE

30. **La Sirena, Coquimbo.**—Type locality of *griseoflavus* Philippi.
30. Romero, Coquimbo.—C. C. Sanborn.
31. **Coquimbo, Coquimbo.**—Type locality of *darwini* Waterhouse; C. Darwin.
32. Fray Jorge, Coquimbo.
33. **Illapel, Coquimbo.**—Type locality of *illapelinus* Philippi.
34. **Choapa, Coquimbo.**—Type locality of *campestris* Philippi.
35. Alicahue, Aconcagua.—J. A. Wolffsohn.
36. Longotoma, Aconcagua.—J. A. Wolffsohn at 200 meters.
37. **La Ligua, Aconcagua.**—Type locality of *platytarsus* Philippi; C. C. Sanborn.
38. Papudo, Aconcagua.—J. A. Wolffsohn at 100 meters; C. S. Reed; C. C. Sanborn.
39. Los Agostinos, Aconcagua.—J. A. Wolffsohn.
40. Las Rojas [=Lo Rojas], Quillota, Valparaiso.—J. A. Wolffsohn at 150 meters.

Explanation of Figure 75 (*continued*)

41. Buen Retiro, Valparaiso.—J. A. Wolffsohn at 250–300 meters.
41. Las Hijuelas, Valparaiso.
41. La Calera, Valparaiso.—J. A. Wolffsohn; C. S. Reed.
42. Palmilla, Valparaiso.—J. A. Wolffsohn at 300 meters.
43. Olmué, Valparaiso (152 meters).—J. A. Wolffsohn.
44. Quilpué, Valparaiso.—J. A. Wolffsohn at 100 meters.
45. Valparaiso, Valparaiso.
46. La Laguna, Valparaiso.
47. Batuco, Santiago.
48. San Cristobal, Santiago.—F. C. C. Platt.
48. Santiago, Santiago.
49. Puente Alto, Santiago.
50. Peñalolen, Santiago.
51. **Angostura, Santiago.**—Type locality of *Mus melanonotus* Philippi.
52. Paine, Santiago; see Peine.
52. **Peine, Santiago.**—Type locality of *dichrous* Philippi and *segethi* Philippi.
53. Pilen Alto, Maule (250 meters).—J. A. Wolffsohn; C. C. Sanborn.
54. Quirihue, Nuble.—C. C. Sanborn.
54. **Coroney Ranch, Nuble.**—Type locality of *boedeckeri* Osgood; C. C. Sanborn.

Phyllotis darwini fulvescens (55)

CHILE

55. **Piedra de Aiguilas, Sierra Nahuelbuta, Malleco.**—Type locality of *fulvescens* Osgood; W. H. Osgood at 4000 feet.
55. Araucaria forest, Nahuelbuta, Malleco.—H. E. Anthony and G. Ottley at 3700 feet.

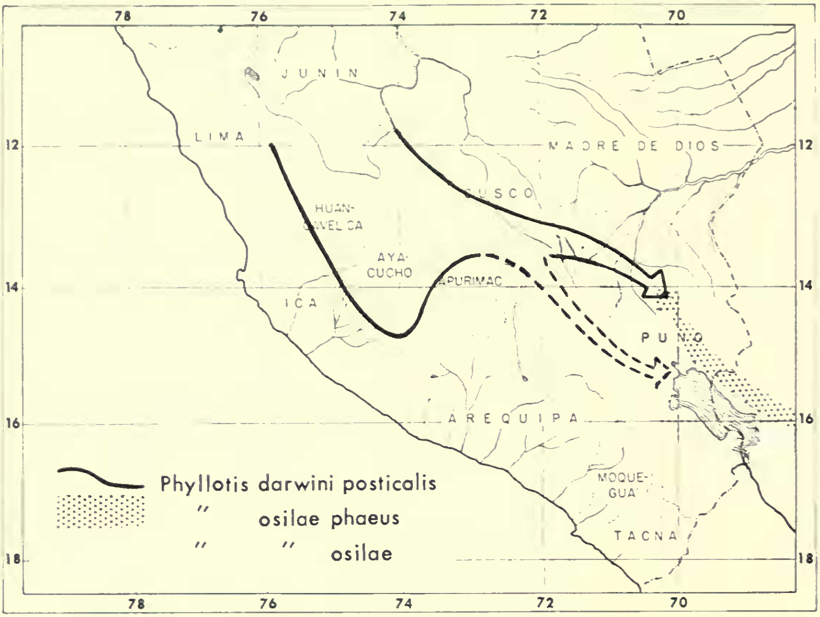
Phyllotis darwini xanthopygus (56–68)

ARGENTINA

56. Pilcañeu, Río Negro.—E. Budín at 1400 meters; H. E. Box.
57. Huanuluan, Río Negro.—J. L. Peters at 3200–3600 feet.
58. Tecka, Chubut.—H. E. Box.
59. Pico Salamanca, Comodoro Rivadavia.
60. Caprek Aike, Comodoro Rivadavia.—C. Burmeister.
61. Basaltic Canyons (Arroyo Aike), Santa Cruz.—O. A. Peterson.
62. Swan Lake (=Lago de Los Cisnes), Santa Cruz.—O. A. Peterson.
62. Arroyo Aike, see Swan Lake and Basalt Canyons.—A. E. Colburn.
63. Río Chico (upper), Santa Cruz.—O. A. Peterson; A. E. Colburn.
64. Lago Viedma, Santa Cruz (225 meters).—J. R. Pemberton.
65. Puerto Deseado, Santa Cruz.—C. Darwin.
65. Port Desire, see Puerto Deseado.
66. **Santa Cruz, Santa Cruz.**—Type locality of *xanthopygus* Waterhouse; C. Darwin; B. Brown, 30 miles south.
67. Río Coig, Santa Cruz.—O. A. Peterson.
67. Río Coy, see Río Coig.

CHILE

68. Laguna Lazo, Magallanes.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76
74
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12
14
16
18
JUNIN
LIMA
MADRE DE DIOS
CUSCO
HUAN-
CAVELICA
AYA-
CUCHO
APURIMAC
ICA
PUNO
AREQUIPA
MOQUE-
GUA
TACNA
Phyllotis darwini posticalis
″ osilae phaeus
″ ″ osilae

FIG. 76.—Contact between *Phyllotis osilae* and *P. darwini posticalis*. Probable origin of *P. osilae* from the ancestral form of *P. darwini posticalis* indicated by broken-lined arrow.

EXPLANATION OF FIGURE 77

Phyllotis osilae: locality records and collectors.

Type localities in **boldface.**

Phyllotis osilae osilae (1–37)

PERU

1. Occobamba, Cusco.—E. Heller at 9500 feet.
2. Macchu Picchu, Cusco.—E. Heller at 12,000–14,000 feet.
3. Ollantaytambo, Cusco.—E. Heller at 13,000 feet.
4. Huarocondo, Cusco.—E. Heller at 10,850 feet.
5. Urco, Cusco.—J. M. Schmidt at 9500–10,000 feet.
6. Santa Rosa de Ayaviri, Puno.—O. P. Pearson at 12,800 feet.
7. Osilla, Puno. = Asilla.
7. **Asillo, Puno.**—H. H. Keays at 12,000 feet; C. B. Koford at 13,000 feet.
8. Tirapata, Puno (3880 meters).—H. H. Keays.
9. Azángaro, Puno (3859 meters).—Ortiz de la Puente at 4020 meters.
10. Checayani, Puno.
11. Calacala, Puno.—C. B. Koford at 13,000 feet.
12. Arapa, Puno.—M. and C. B. Koford at 12,600 feet.
13. Umayo, Puno.—M. Koford at 12,700 feet.
14. Isla Amantí, Lago Titicaca, Puno.
15. Vilque, Puno.—O. P. Pearson at 13,300 feet.

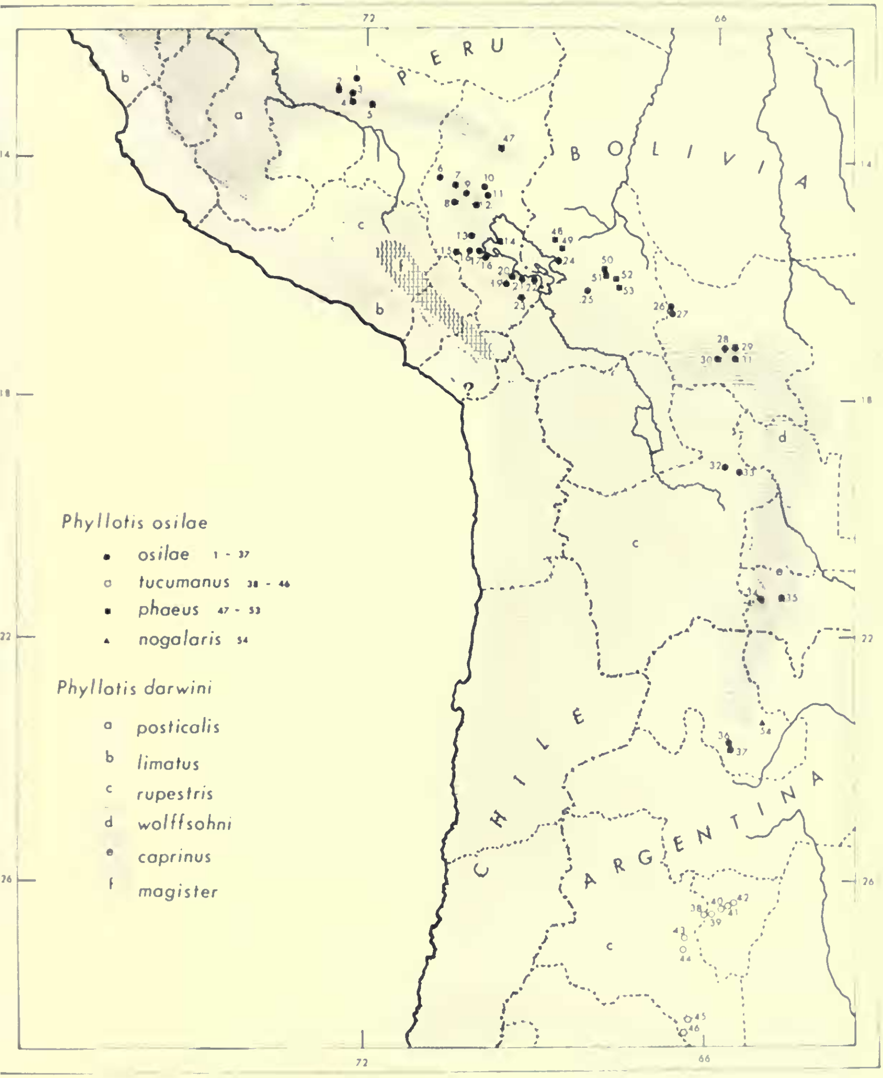
PERU
BOLIVIA
CHILE
ARGENTINA
Phyllotis osilae
● osilae 1 - 37
○ tucumanus 38 - 46
■ phaeus 47 - 53
▲ nogalaris 54
Phyllotis darwini
a posticalis
b limatus
c rupestris
d wolffsohni
e caprinus
f magister
72
66
14
18
22
26
?

FIG. 77.– Collecting localities of the subspecies of *Phyllotis osilae*. Shaded areas show approximate ranges of the subspecies of *Phyllotis darwini* in southern Peru, Bolivia, and northern Argentina and Chile. See opposite page for explanation.

Explanation of Figure 77 (*continued*)

16. Occomani, Puno.—C. C. Sanborn at 12,700 feet.
17. Puno, Puno (3822 meters).—A. K. and O. P. Pearson at 13,000 feet; M. C. Portugal.
18. Chucuito, Puno.—C. C. Sanborn at 12,800 feet.
19. Pairumani, Puno.—C. B. and M. Koford at 13,000 feet; A. K. and O. P. Pearson at 12,800 and 13,500 feet.
20. Juli, Puno.—A. K. Pearson at 12,700 feet.
21. Pomata, Puno.—A. K. and O. P. Pearson at 12,500 feet.
22. Yunguyo, Puno.—C. C. Sanborn at 13,000 feet.
23. Huacullani, Puno.—C. C. Sanborn at 12,700 feet.

BOLIVIA

24. Achacachi, La Paz.—R. M. Gilmore at 3800 meters.
25. La Paz, La Paz (3720 meters).
26. **Choro, Cochabamba.**—Type locality of *lutescens;* P. O. Simons at 3200–3500 meters; F. Steinbach at 3500 meters.
27. Choquecamate, Cochabamba.—P. O. Simons at 4000–4300 meters.
28. Colomi, Chaparé, Cochabamba.—F. Steinbach.
29. Tiraque, Cochabamba.—Collected at 15 miles ESE.; O. P. Pearson at 10,500 feet.
30. Punata, Cochabamba.—Collected 10 miles NE.; O. P. Pearson at 10,500 feet.
31. Vacas, Cochabamba.—J. Steinbach at 3800 meters.
32. Lagunillas, Potosí (3500 meters).—P. O. Simons.
33. El Cabrado, Potosí.—P. O. Simons at 3500 meters.
34. Tarija, Tarija.—Collected 10 miles NW.; O. P. Pearson at 8200 feet.
35. Pinos, Tarija.—E. Budín at 1700 meters.

ARGENTINA

36. León, Jujuy.—E. Budín at 1500 meters; O. P. Pearson at 5800 feet.
37. Yala, Jujuy, mountains west of.—W. H. Osgood at 10,000 feet.

Phyllotis osilae tucumanus (38–46)

ARGENTINA

38. Ciénaga, Tucumán.
39. Tafi del Valle, Tucumán.—L. E. Miller and H. S. Boyle at 7000 and 9500 feet.
40. **Cumbre de Mala Mala, Sierra de Aconquija, Tucumán.**—Type locality of *tucumanus;* E. Dinelli at 3300 meters.
41. Cerro San Javier, Tucumán.—E. Budín at 2000 meters.
42. Ñorco, Vipos, Tucumán.—E. Budín at 1500–2000 meters.
43. Aconquija, Catamarca.—J. Mogensen at 3000 meters.
44. Río Vallecito, Andalgalá, Catamarca.—J. Crespo at 2900 meters.
45. Otro Cerro, Catamarca.—E. Budín at 3000 meters.
46. Chumbicha, Catamarca.—E. Budín at 500–600 meters.

Phyllotis osilae phaeus (47–53)

PERU

47. **Limbani, Puno.**—C. C. Sanborn at 11,000 feet; C. B. Koford at 11,500 and 13,000 feet.

Explanation of Figure 77 (*continued*)

BOLIVIA

48. Sorata, La Paz (2657 meters).—H. E. Anthony and G. Ottley.
49. Tacacoma, La Paz.—H. E. Anthony and G. Ottley.
50. Alaska Mine, La Paz.—G. H. H. Tate at 13,700 feet.
51. Pongo, La Paz.—G. H. H. Tate at 12,000 feet.
52. Aceramarca, La Paz.—G. H. H. Tate at 10,800 feet.
53. Yanacachi, La Paz.

Phyllotis osilae nogalaris (54)

ARGENTINA

54. **Higuerilla, Valle Grande, Jujuy.**—E. Budín at 2000 meters.

The Species of the Phyllotis darwini Complex

Four species are recognized. They are so closely related *inter se* that if large series from certain crucial areas had not been available for study, the four might well have been regarded as one. There is a probability, nevertheless, that even more material from as yet unexplored regions may reverse this conclusion and prove that all members of the *P. darwini* group are still intergrading segments of a single species.

A key to the species based on morphology alone would not be feasible, if at all possible. The key devised by Pearson (1958, pp. 407–408) to all species of the genus *Phyllotis* depends largely and, in critical areas, entirely, on geographic data. This is extreme and prejudices taxonomic judgments. Only the species of the *darwini* complex lack trenchant diagnostic characters. The members of the group, however, are mostly or wholly allopatric to each other. Several occupy parts of a geographic gradient in size and some differ in proportion of parts and the shape of the baculum. These considerations are combined in the following "key" to the species.

1. *Phyllotis haggardi.*—Andes of Ecuador. Size small; tail short-haired, less than 95 mm. and always shorter than head and body combined.
2. *Phyllotis andium.*—Andes of Ecuador and Peru as far south as Lima. Average size greater than *haggardi;* tail short-haired and more than 95 mm. or longer than head and body combined; base of baculum convex or plane (*osilae* type, fig. 7).
3. *Phyllotis darwini.*—Peru from Junín and Lima departments south into Bolivia, Chile and Argentina. Average size greater than *andium;* tail short- or long-haired and longer or shorter than head and body combined; base of baculum concave or plane (*darwini* type, fig. 7).
4. *Phyllotis osilae.*—Andes of southern Peru (Cusco-Puno), Bolivia, northern Argentina; size and proportions as in *P. darwini;* tail short-haired; ears usually less than 23 per cent of head and body; m^{2-3} with first primary fold obsolete or absent in moderately worn tooth; second primary fold of m^3 nearly always an enamel island; base of baculum convex or plane (*osilae* type, figs. 7, 86).

Phyllotis haggardi Thomas

Phyllotis haggardi Thomas, 1898, Ann. Mag. Nat. Hist., (7), **2**: 270. Thomas, 1912, op. cit., (8), **10**: 409–410—comparisons. Lönnberg, 1913, Ark. Zool., Stockholm, 8, (16): 27—*Pichincha* (Mt. Pichincha; Quito). Stone, 1914, Proc. Acad. Nat. Sci. Phila., p. 11—*Pichincha* (Hacienda Garzón, Mt. Pichincha, 12,000 ft.). Allen, 1916, Bull. Amer. Mus. Nat. Hist., **35**: 120—*Pichincha* (Mt. Antisana, 12,000 ft.). Pearson, 1958, Univ. California Publ. Zool., **56**: 441—characters; comparisons.

Phyllotis haggardi haggardi, Pearson, 1958, Univ. California Publ. Zool., **56**: 442—*Imbabura* (Mt. Mojanda); *Pichincha* (Guaillabamba; Imbuyo; Jerusalén; La Providencia; Perucho; Puellaro; Puembo; Tanda; Ventanilla; Quito; Mt. Pichincha); characters; comparisons; distribution.

Hesperomys elegans, Tomes (not Waterhouse), 1860, Proc. Zool. Soc. London, **1860**: 213—*Chimborazo* (Pallatanga).

Phyllotis elegantulus Thomas, 1913, Ann. Mag. Nat. Hist., (8), **11**: 139—type locality Pallatanga, Chimborazo Province, Ecuador.

Phyllotis haggardi elegantulus, Pearson, 1958, Univ. California Publ. Zool., **56**: 443—status of type.

Phyllotis fuscus Anthony, 1924, Amer. Mus. Nat. Hist. Novit., no. 114: 1—type locality Contrayerbas, Azuay, Ecuador, 11,000 ft. Goodwin, 1953, Bull. Amer. Mus. Nat. Hist., **102**: 324—history of type; measurements.

Phyllotis haggardi fuscus, Pearson, 1958, Univ. California Publ. Zool., **56**: 442—*Azuay* (Contrayerbas); *Chimborazo* (Mt. Chimborazo; Urbina); *Pichincha* ("Galaya" [=Saloya]; Guamaní; Mt. Antisana; Mt. Corazón, *Cotapaxi* (Mt. Illiniza); *Napo-Pastaza* (Papallacta); characters; comparisons; distribution.

Type.—Skin and skull, sex unknown, British Museum (Natural History) no. 98.5.1.11; collected October 1897, by Ludovic Söderström.

Type locality.—Mt. Pichincha, above Quito, Pichincha Province, Ecuador; altitude, 3400–4000 meters.

Distribution (figs. 70–72).—Andes of Ecuador, from just north of the Equator to about 3° 30′ south in the Province of Azuay; altitudinal range from approximately 2000 to over 4000 meters above sea level.

External characters.—Smallest species of the *P. darwini* complex; tail less than 95 millimeters and shorter than combined head and body length; ears short, apparently less than 23 per cent of combined head and body length; upper parts of body buffy to dark brown with head and rump not markedly different from back; under parts gray, well defined from sides, a minute pectoral streak rarely present; tail bicolor, short-haired, pencil little developed.

Cranial characters (figs. 78, 79).—Interorbital region narrow, parallel-sided or, usually, concave mesially, the edges square; proximal ends of nasals usually pointed and terminating behind plane of frontopremaxillary sutures; posterolateral palatal fossa well excavated, the pits large and usually situated anteriad to plane of posterior border of palate; antero-posterior length of bulla, less tube, subequal to alveolar length of molar row.

Dental characters.—Generally as in *P. darwini;* alveolar length of molar row, 3.9–5.0 (49 specimens).

Comparisons.—Phyllotis andium is the only closely related species found in or near the range of *P. haggardi.* It is distinguished by longer tail and cranial characters described under the species heading. Comparisons with other species are made elsewhere (p. 263).

Variation.—Pale and dark populations are scattered throughout the range of the species. As a rule, dark populations occur at the altitudinal peaks of the range, i.e., on the high humid grasslands, or *páramos,* of Mounts Pichincha, Mojanda, Corazón, Antisana, etc., from 3500 meters to more than 4000 meters above sea level. Most of these dark populations are isolated from each other. Pale populations are found at the opposite altitudinal extremes, in the isolated arid and semi-arid intermontane valleys, between 200 and 2500 meters above sea level. Dark and pale populations grade insensibly into each other, or into the main population mass occupying the broad and continuous intermediate altitudinal zone.

There is an increase in size and relative length of tail from north to south. Because of the uneven topography and the great diversity of local environments, the gradient is correspondingly uneven, obscured at some points and disrupted at others.

Although recognizing the cline in size, bodily proportions and color, Pearson (1958, pp. 441–443) admitted three subspecies of *Phyllotis haggardi.* The nominate form was restricted to the type locality in the Pichincha-Quito area, thence northward about 30 miles to Mt. Mojanda. *P. h. elegantulus* was recorded from its type locality only in Pallatanga, Chimborazo, while the range of *fuscus* engulfed those of the other two. A specimen in Chicago Natural History Museum from Saloya, misspelled "Galaya" on the museum label, was referred by Pearson to *fuscus* on the assumption it originated in the province of Chimborazo. Actually, Saloya lies west of Mt. Pichincha in Pichincha province. The Saloya specimen was taken by F. Mena. Two specimens from Chimborazo, in Chicago Natural History Museum, were also collected by A. Mena.

Taxonomy.—Phyllotis haggardi was originally characterized as "The Ecuadorean [sic] representative of the Chilian *Ph. darwini* . . . distinguished by its smaller size and smaller ears." Present material confirms the smaller size of *haggardi.* Collectors' ear measurements are not available for the vast majority of the specimens examined. The ears, however, do appear to average smaller in proportion to head and body length than those of most members of the group. The type, collected by Söderström, is an imperfect specimen with incomplete skull and without the usual collector's data. Its published external measurements were taken from the dry skin. Specimens at hand include 79 individuals from the type region, also collected by Söderström. Most of them are juvenals and subadults. The color and texture of many skins indicate undue exposure to drying and fading. No external measurements are given and accurate ones cannot be made on the distorted specimens. There is considerable mismatching between skins and skulls of the same species while some skins are coupled with skulls of mice of the genera *Akodon*, *Thomasomys* and *Reithrodontomys*. It is assumed that data given on the original labels of some of these Söderström specimens are likewise untrustworthy.

Phyllotis elegantulus Thomas, from Pallatanga, Chimborazo Province, was described as "a small species allied to *Ph. amicus*, but with shorter tail." The type was skinned out of spirits and the original description is based on the dried, made-up skin. Color of the type, said to be "somewhat modified . . . but apparently as in *Ph. amicus*," agrees as well with that of *Phyllotis haggardi*. External measurements and cranial characters given by Thomas for distinguishing *elegantulus* from *amicus* are precisely those that distinguish *haggardi* from *amicus*. Present material from the type region of *elegantulus* is unquestionably representative of *haggardi*. Pearson (1958, p. 443), who examined the type and what appeared to be a topotype, confirmed the identification of *elegantulus* with the nominate form of *haggardi* rather than with *fuscus*. He, nevertheless, retained *elegantulus* as a valid subspecies, chiefly to avoid placing the "clearly defined *P. h. fuscus* into synonymy under the almost unknown *elegantulus*."

Phyllotis fuscus Anthony, from Contrayerbas, Azuay Province, Ecuador, was distinguished from topotypes of *haggardi* by darker color and longer rostrum. The Contrayerbas series at hand does average darker than Mt. Pichincha and Quito *haggardi*, but the difference is local, if not seasonal. A large series of *Phyllotis* from Mt. Antisana just southeast of Quito also averages darker than topotypes of *haggardi* and is quite as dark as the Contrayerbas *Phyllotis*. The longer rostrum attributed to *fuscus* as compared with topotypes of *haggardi* merely reflects the increase in size of the species from north to south. The proportions of the parts, however, remain practically the same, as shown in Table 11. Specimens listed are those of fully mature adults with skulls in good condition.

TABLE 11.—Measurements of topotypes (Mt. Pichincha) of *Phyllotis haggardi* Thomas and topotypes (Contrayerbas) of *Phyllotis fuscus* Anthony

Locality	Specimen no.	Greatest length of skull	Nasal length	Ratio %
Mt. Pichincha[1]	CNHM 53305	26.5	11.7	44
”	MACN 31150	26.7	11.3	42
”	” 31151	25.7	11.3	44
”	AMNH 46825	26.6	10.8	40
”	” 46826	26.2	10.5	40
”	” 46829	26.5	11.3	43
”	” 46836	27.0	11.6	43
Contrayerbas[2]	AMNH 62050[3]	29.5	12.6	43
”	” 61957	29.0	12.3	42
”	” 61959	28.7	12.4	43
”	” 61960	28.3	11.5	40
”	” 61961	28.7	11.0	38

[1] Means and extremes of nasal length of 11 specimens measured by Pearson (1958, p. 465), 10.93±0.14 (10.4–11.7).

[2] Means and extremes of nasal length of 5 specimens measured by Pearson (1958, p. 465) 12.34±0.12 (12.0–12.6). The difference of 1 millimeter in the minimum length of the nasals in the two sets of measurements does not affect the conclusions. If nasals of no. 61961 were 12.0, the ratio would be 42%.

[3] Type of *Phyllotis fuscus* Anthony; measurements from original description.

Measurements.—See Table 12.

Specimens examined.—124, all from Ecuador. *Pichincha:* Mt. Pichincha and vicinity including Quito, 49 (AMNH, 40; CNHM, 4; MACN, 2; MCZ, 3); Mt. Mojanda, 12 (AMNH); south slope of Mt. Mojanda and vicinity of Guaillabamba, 7 (AMNH); Río Guaillabamba, 1 (AMNH); Jerusalén, Guaillabamba, 4 (AMNH); Puellaro, 6 (AMNH); Puembo, 1 (AMNH); Jirón, 1 (AMNH); Saloya, 1 (CNHM); Mt. Antisana, 16 (AMNH, 13; MCZ, 3); Mt. Corazón, 12 (AMNH). *Cotapaxi* (formerly León): Mt. Illiniza, 1 (MCZ). *Napo-Pastaza:* Papallacta, 1 (AMNH). *Chimborazo:* Urbina, 1 (AMNH); Mt. Chimborazo, 3 (CNHM). *Azuay:* Contrayerbas, 8 (AMNH).

Phyllotis andium Thomas

Phyllotis andium Thomas, 1912, Ann. Mag. Nat. Hist., (8), **10**: 409. Osgood, 1914, Field Mus. Nat. Hist., Zool. Ser., **10**: 165—*Cajamarca* (Hacienda Limón near Balsas; Hacienda Llagueda); *Libertad* (mountains near Otuzco). Thomas, 1926, Ann. Mag. Nat. Hist., (9), **18**: 162—*Amazonas* (Condechaca; Chachapoyas; Molinopamba). Thomas and St. Leger, 1926, op. cit., (9), **18**: 348—*Amazonas* (Goncha). Pearson, 1958, Univ. California Publ. Zool., **56**: 408, 440—characters; comparisons; distribution [for locality records see explanation of figs. 71, 72]; synonyms, *melanius, stenops, tamborum, fruticicolus.*

TABLE 12.—Measurements of *Phyllotis haggardi* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
Guaillabamba	—	—	—	—	26.6	—	4.3
Pichincha[1]	97	86	23	18	—	13.5	4.4
Pichincha	105(97-115)5	75(68-85)5	23(22-24)5[2]	—	26.5(26.2-27)8	13.9(13.5-14.6)8	4.6(4.3-4.9)9
Saloya	110	75	—	—	—	—	4.5
Papallacta	—	—	—	—	27.3	14.4	4.4
Corazón	—,—	—,—	—,—	—,—	25.9,26.7	—,—	4.1,4.2
Antisana	100,99,104	68,74,74	23,24,22	—,—,—	26.7,27.6,27.7	14.1,14.4,15.0	4.4,4.2,4.2
Chimborazo	91,114,118	69,66,60	24,23,24	20,20,22	—	14.2,—,—	4.6,4.3,4.7
Urbina	105	73	24	—	27.4	15.1	4.4
Pallatanga[3]	92	70	21	17	27	—	4.0
Contrayerbas[4]	113	85	27	—	29.5	15.0	4.3
Contrayerbas	113,102,111,110	85,88,89,88	27,27,26,26	—,—,—,—	28.3,28.7,28.7,29.0	14.9,14.6,14.9,15.1	4.6,4.6,5.0,4.6

[1] Type of *haggardi;* measurements from original description (external measurements from dry skin).

[2] Dry, with claw.

[3] Type of *elegantulus;* measurements from original description (external measurements from dry skin of specimen originally preserved in spirits).

[4] Type of *fuscus;* measurements from original description.

P[hyllotis] andium, Thomas, 1926, Ann. Mag. Nat. Hist., (9), **17**: 615—*Amazonas* (Chachapoyas); *stenops* a synonym.

[Phyllotis lutescens] andium, Osgood, 1944, Field Mus. Nat. Hist., Zool. Ser., **29**: 194—classification.

Phyllotis melanius Thomas, 1913, Ann. Mag. Nat. Hist., (8), **11**: 407—part, skull only; ECUADOR: (type locality Porvenir, Bolívar, 1800 meters). Pearson, 1958, Univ. California Publ. Zool., **56**: 440—type a composite of skull of *Phyllotis andium* from Cañar and skin of *Akodon aerosus* from Porvenir; type restricted to skull only.

Phyllotis andium stenops Osgood, 1914, Field Mus. Nat. Hist., Zool. Ser., **10**: 165—PERU: (type locality Río Utcubamba, 15 miles above Chachapoyas, Amazonas, altitude, 7500 feet).

Phyllotis tamborum Osgood, 1914, Field Mus. Nat. Hist., Zool. Ser., **10**: 165—PERU: (type locality Tambo Carrizal, east of Balsas, Amazonas).

Phyllotis andium tamborum, Thomas, 1926, Ann. Mag. Nat. Hist., (9), **17**: 614—PERU: *Cajamarca* (Celendín); *Amazonas* (Tambo Carrizal; Leimabamba).

Phyllotis fruticicolus Anthony, 1922, Amer. Mus. Nat. Hist., Novit., no. 32: 1—ECUADOR: (type locality Guachanamá, Loja, Ecuador, 9050 ft.). Goodwin, 1953, Bull. Amer. Mus. Nat. Hist., **102**: 323—history of type; measurements.

Phyllotis darwini posticalis, Thomas (not Thomas), 1927, Ann. Mag. Nat. Hist., (9), **20**: 602—PERU: *Huánuco* (Llata); *Pasco* (Huariaca); *Ancash* (Pira).

Type.—Adult male, skin and skull, British Museum (Natural History) no. 99.9.9.68; collected 18 April, 1899, by Perry O. Simons.

Type locality.—Cañar, Cañar Province, Ecuador; altitude, 2600 meters.

Distribution (figs. 70–72).—From Tungurahua Province in the Andes of central Ecuador south through the Andean departments of Peru between the coastal and Río Huallaga drainage basins as far as northern Junín and western Lima; altitudinal range from approximately 200 to 4800 meters above sea level.

External characters.—Average size larger than *P. haggardi*, smaller than *P. darwini;* tail 95 millimeters or longer and usually (always in Ecuador) longer than combined head and body length; ear, from notch, 25 millimeters or less; upper parts nearly uniformly warm brown; sometimes buffy or slightly grizzled but with little or no contrast between anterior third and posterior parts of body; underparts gray, often with a thin wash of pale buff; a poorly defined pectoral patch or streak rarely present; tail short-haired with poorly developed pencil, sharply bicolor but tip often uniformly brown.

Cranial characters.—Interorbital region parallel-sided, or, usually, concave mesially, the edges square, never beaded or forming ledges, the median frontal sulcus weakly defined or absent; proximal ends of nasals usually truncate and terminating approximately in line with fronto-premaxillary sutures; posterolateral palatal fossa poorly defined, the pit (or pits) large or small and situated on a line with, or, usually, anteriad to, plane of posterior border of palate; posterior border of palate round or square and with or without median cleft or median process; width of mesopterygoid fossa, measured at base of hamular processes subequal to or less than width of parapterygoid fossa measured at same plane, sides parallel or slightly concave medially, sometimes slightly divergent; bullae moderately inflated, antero-posterior length, less tubes, 3.8–4.8 and always less than alveolar length of molar row; auditory bullae comparatively little inflated, Eustachian tubes short to moderately elongate.

Dental characters.—Generally as in the *P. darwini* group but m^2 more often S-shaped than 8-shaped, *pf* 1 of m^2 more often absent or obsolete in moderately worn tooth, *pf* 2 of m^3 nearly always an enamel island; molar rows parallel or slightly convergent posteriorly; alveolar length 4.1–5.3 (190 specimens).

Baculum.—See discussion on p. 58 and figures 7 and 8.

Comparisons.—Two species and three subspecies of the *Phyllotis darwini* complex occur in or near the range of *P. andium.* The Ecuadorian *P. haggardi* is slightly smaller with tail actually and proportionately shorter. *P. darwini posticalis* and *P. d. limatus* average larger throughout with bullae usually more inflated. *P. d. definitus* is absolutely larger with molars larger, body more warmly colored throughout, the under parts washed with ochraceous, pectoral patch well defined.

Separation of *Phyllotis andium* from *P. haggardi* and *P. darwini posticalis* is not always clear. Evidently, speciation was recently accomplished and only in critical geographic areas is it sufficiently defined for recognition. Specific distinction between *P. andium* and *P. darwini posticalis* is predicated principally if not solely, on the basis of a small series of each species collected by Pearson near Casapalca, Lima, Peru. Here the representatives of the two species differ in virtually all dimensions, notably in inflation of bullae and proportional width of interorbital region (Table 13). Some of these differences may be age factors, the *andium* series being younger. The *posticalis* series, however, is also darker, more gray, with a coarser ticking, has more prominent guard hairs, hairier tail and its median palatal spine is poorly defined or absent.

TABLE 13. —Measurements of *Phyllotis andium* and *P. darwini posticalis* from Casapalca, Lima, Peru

	Head and body	Tail	Hind foot (dry)	Ear	Ear: head and body	Greatest skull length	Interorbital width	Interorbital: skull length	Length of auditory bullae	Nasals	Nasals: skull length	Alveolar row	Alveolar row: skull length	Palatal spine
CASAPALCA, LIMA														
andium														
M 120010 s	100	112	25	20	20	27.0	4.3	16	4.3	10.8	40	4.7	17	present
M 120011 s	99	114	26	20	20	27.7	4.4	16	4.3	11	40	4.8	17	”
M 120012 s	98	119	26	20	20	27.5	4.2	16	4.5	11	40	5.0	18	”
M 120013 j	97	110	26	21	22	27.2	4.4	16	4.4	10.6	39	4.9	18	”
darwini														
M 120085	121	127	27	24	20	32	4.4	14	4.8	13.3	41	5.6	17	absent
M 120086	126	126	29	25	20	31.2	4.4	14	5.1	12.9	41	5.7	18	”
M 120087	116	124	27	26	22	30.6	4.6	15	4.9	12.4	40	5.4	18	”
M 120088 s	101	109	26	24	24	28.5	4.4	15	4.9	11.0	38	5.1	18	”

M = catalog number of specimen in Museum of Vertebrate Zoology.
s = subadult.
j = juvenal.

Specimens of *darwini* and *andium* from other localities in the area of sympatry are imperfect for comparative purposes. One specimen of *Phyllotis darwini limatus* (MVZ 120033) from Surco, Lima, is a hydrocephalous juvenal with an abnormally inflated braincase (fig. 80,*a*). Its skull cannot be fairly compared with those of three adult *andium* from the same locality. However, external differences between the Surco *darwini* and sympatric *andium* are the same as obtain between the two Casapalca species except that the tail of *darwini* is not appreciably longer-haired. One specimen of *P. darwini limatus* from 1 mile east of San Bartolomé is also pale, with a more coarsely ticked coat and slightly hairier tail as compared with a series of 10 specimens of *andium* from the same locality. The *andium* series also shows well the shorter and broader muzzle, less inflated bullae and other distinguishing cranial characters of the species.

Some allopatric series of *andium*, notably one from Chongoyape, Lambayeque, differ even more widely from the sympatric series of *posticalis* while others overlap in all characters except relative degree of inflation of the bullae. The slight but real difference in the auditory bullae is fairly constant throughout the geographic range of both species. Unfortunately bullae cannot be accurately compared in terms of the linear measurements used here.

Evidence of sympatry between *P. andium* and *P. haggardi* is lacking. Both species become larger, their tails longer, from north to south. The size cline in *andium* begins along the same coordinate south of the point where the known range of *haggardi* ends. On the other hand, *P. andium* remains nearly the same size with the same long tail where its range parallels that of *P. haggardi*. This phenomenon is the dubious basis for specific separation of the two forms. Cranial characters used by Pearson (1958, p. 437) for distinguishing *haggardi* from *andium* include "longer palate, posteropalatal pits usually sunk in depressions, tooth rows tending to converge posteriorly, zygomatic arches more widely flaring." These characters though valid in present material are of the kind which in larger samplings usually prove to be local or individual variables.

The less nearly related *Phyllotis amicus* is smaller, with longer tail, larger ears, skull with broad divergent-sided supraorbital region, incisors more delicate and m^2 with procingulum more developed.

Variation.—The various series of *andium* from the Department of Lima are fairly uniform in cranial characters, notably in the presence of a well-developed median spine on the posterior border of the palate. This feature is insignificant or absent in the vast majority of *andium* from elsewhere. Specimens from localities in Lima coincident with or near the range of dark-colored *Phyllotis darwini posticalis* are dark, others from paler *Phyllotis darwini limatus* territory (Surco, Santa Eulalia) are correspondingly paler.

A series of 36 specimens from Macate, northern Ancash, taken from 1 February through 6 March, 1914, by M. P. Anderson, is more brown, on an average, than *andium* from the Department of Lima. A series from Yungay, Ancash, collected March 4–6, 1954, southeast of Macate, is more somberly colored because all 11 specimens are in old, worn pelage. Nevertheless, patches of new pelage on the dorsum of one specimen (CNHM 81246) are colored as in the Macate series. Thirty-three specimens from Huaras, Quilcayhuanca and Hacienda Catac, in the Department of Ancash, are paler than those from Yungay. They were taken in February 1954. All are in old pelage, but some show patches of new pelage. None compare with the Macate specimens which are in prime pelage although taken in the same general region during the same month 40 years earlier. The series from Huaras includes individuals nearly as pale as coastal *Phyllotis darwini limatus*.

Eight small, pale, long-tailed mice from Chongoyape, Lambayeque, a locality 240 meters above sea level on the coast of northern Peru, closely resemble large individuals of the nearly related *Phyllotis amicus*. This population may represent a desert race characterized by small size, extremely pale color and long tail. In most of the Chongoyape specimens the molar crowns are considerably worn, the dentine deeply excavated. As noted elsewhere, unusually small size appears to be correlated with excessive molar wear. Evidently, in the Chongoyape ambience the mice were obliged to feed on tough-fibered plants with low nutritional value.

Taxonomy.—The type of *Phyllotis andium stenops* Osgood, from Río Utcubamba, Chachapoyas, is the only fully mature individual of a series of ten from the Chachapoyas area in southern Amazonas. The series was distinguished from Cajamarca representatives of *andium* "principally by the narrowness of [the] nasals." It has already been shown by Thomas and Pearson that subspecific distinction of *stenops* by this or any other character is untenable.

The type of *Phyllotis tamborum* Osgood, from the mountains east of Balsas, southeast of Chachapoyas, is a juvenal absolutely indistinguishable from Chachapoyas *stenops*.

Phyllotis fruticicolus Anthony, from Guachanamá, southern Ecuador, is, as shown by Pearson (1958, p. 441), indistinguishable from

TABLE 14.—Measurements of *Phyllotis andium* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
ECUADOR							
Punín	88,88,94,102	90,92,108,112	23,23,25,26	—,—,—,—	—,—,26.8,27.7	—,—,13.5,14.0	4.4,4.4,4.5,4.9
Cañar[1]	115	119	25	21	28.7	15.2	4.4
Yunguilla Valley	90,100,100	100,100,70	25,24,25	30	—,—,—	—,—,—	4.8,4.6,—
Guachanamá[2]	91	102	24	—	24.7	12.4	4.2
Guachanamá	84	99	23	—	26.6	12.4	4.1
PERU							
Chongoyape	101(87-114)8	117(108-132)8[3]	24(23-26)8	21(21-22)8	26.2(24.9-27.6)8	13.3(12.2-14.4)8	4.3(4.1-4.6)8
Cabache	97	115	25	22	26.5	13.0	4.6
Huancabamba	125,120	108,110	26,26	22,22	28.1,29.9	13.9,14.4	4.8,5.0
Chachapoyas[4]	117	132	26	—	29.4	14.5	5.0
Chachapoyas	109,116	127,121	24,25	—	27.0,28.0	14.1,14.5	4.9,4.7
Carrizal[5]	99	118	24	—	25.6	12.8	4.6
San Pedro	110,105	92,123	26,24	—,—	28.2,28.6	14.7,14.6	4.6,4.6
Cajamarca	115(103-121)8	111(98-121)8[6]	25(24-26)8	—	28.0(27.3-28.4)7	14.1(13.5-14.5)8	4.9(4.6-5.2)8
Limón	112	98	25	—	28.2	14.4	5.2
near Otuzco	114	128	26.5	—	29.0	14.4	5.3
Llagueda	113	131	26.5	—	29.4	—	5.0
Macate ♂♂	114(107-120)7	117(108-124)8[7]	26(25-27)9[8]	—	28.4(27.3-29.5)7	15.0(14.5-15.5)8	4.94(4.7-5.1)8
Macate ♀♀	108(102-122)11	116(104-128)10[9]	26(24-27)11	—	27.9(27.2-29.2)9	14.5(14.1-15.0)8	4.99(4.6-5.2)10
Yungay	118(117-119)5	119(116-123)5[10]	27(26-28)5	21.5(21-22)5	28.8(28.3-30.2)5	15.0(14.6-15.4)5	4.7(4.4-5.0)5
Huaras	115(102-121)14	107(100-128)14[11]	27(26-28)14	21.3(21-22)14	28.4(27.6-29.9)13	15.0(14.5-16.0)14	5.0(4.7-5.2)14
Quilcayhuanca	116(113-127)11[12]	116(107-123)11	26(25-27)11	21.5(21-22)11	28.2(27.4-29.4)11	14.7(14.2-15.6)11	4.8(4.4-5.0)11
Catac	114(104-127)8[13]	114(109-123)8	26(25-28)8	22(21-23)8	27.9(26.8-29.3)8	14.6(14.3-15.3)8	4.8(4.6-5.2)8
Cullcui	106,126	98,122	26,25[8]	—,—	27.6,28.0	13.5,14.2	4.9,4.8

Table 14.—Measurements of *Phyllotis andium* Thomas (*continued*)

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
Matucana	111,114,127	117,122,135	26,26,27	23,—,—	29.3,29.8,30.3	14.8,14.9,15.0	5.2,4.9,5.2
Huarós	98,103,111	106,114,121	26,25,25	22,22,23	27.4,28.8,29.6	14.4,14.2,14.6	4.9,5.3,5.1
Canta	112	110	27	22	29.0	15.0	4.9
Villavista	104(97–118)7	119(107–128)7	26(25–26)7	22(21–23)7	28.1(26.7–30.5)7	14.4(13.8–15.4)7	5.0(4.9–5.3)7
San Mateo	110,106	115,114	26,26	23,23	28.2,28.4	14.6,14.6	5.2,5.0
Zarate	104(94–118)9	120(109–138)9	25(24–26)9	23(21–25)9	28.3(26.8–29.9)9	14.4(13.8–15.1)9	5.0(4.8–5.2)9
Surco[14]	99,105	126,123	26,26	23,22	28.4,28.4	14.6,14.1	4.6,4.5

[1] Type of *andium;* measurements from original description.

[2] Type of *fruticicolus* Anthony; measurements from original description.

[3] Tails of all longer than combined head and body length. Tail: head and body=(110–126):100.

[4] Type of *stenops* Osgood.

[5] Type of *tamborum* Osgood, a juvenal.

[6] Tails of 4 shorter, of 4 longer, than combined head and body length. Tail: head and body=(96–107):100.

[7] In 13 specimens, tails of 7 longer, of 6 shorter than combined head and body length. Tail: head and body=(94–111):100.

[8] Dry, to longest claw.

[9] In 20 specimens, tails of 13 longer, of 5 shorter than combined head and body length, and 2 of equal length. Tail: head and body=(92–118):100.

[10] In 11 specimens, tails of 8 longer, of 2 shorter than combined head and body length, and 1 of equal length. Tail: head and body=(92–111):100.

[11] In 14 specimens, tails of 4 longer, of 8 shorter, than combined head and body length, and 2 of equal length. Tail: head and body=(95–108):100.

[12] In 11 specimens, tails of 3 longer, of 5 shorter, than combined head and body length, and 3 of equal length. Tail: head and body=(96–104):100.

[13] In 8 specimens, tails of 4 longer, of 4 shorter than combined head and body length. Tail: head and body=(94–106):100.

[14] Weight in grams, 33, 31.

andium. The description was based on a comparison of the type, an immature male, and two immature topotypes with *Phyllotis haggardi.*

According to Pearson (1958, p. 440) the name *Phyllotis melanius* Thomas, 1913, is based on a skin of an *Akodon aerosus* and a skull of a *Phyllotis andium.* Skin and skull were collected by P. O. Simons, the former in Porvenir, Bolívar, Ecuador. Both bear Simons' field number 258 and the British Museum (Natural History) number 99.9.9.107. Pearson restricted the name *Phyllotis melanius* to the skull alone. He further demonstrated that a skin only of *Phyllotis andium,* also collected by P. O. Simons and with the same field number, was almost certainly the correct skin of the type skull. Inasmuch as *Phyllotis* does not occur in Porvenir, Ecuador, and the skin with the same field number as the type skull originated in Cañar, Ecuador, the type locality of *melanius* was redetermined as Cañar by Pearson. *Phyllotis melanius* thus becomes a topotype and absolute synonym of *P. andium.*

Measurements.—See Table 14.

Specimens examined.—212. ECUADOR.—*Chimborazo:* Punín, Quebrada Chalán, 4 (AMNH). *Azuay:* Pauijchi, 1 (AMNH); Yunguilla Valley, 7 (CNHM). *Loja:* Guachanamá, 2 including type of *fruticicolus* (AMNH). PERU.—*Piura:* Ayavaca, 1 (CNHM); Huancabamba, 5 (AMNH, 3; CNHM, 2). *Lambayeque:* Chongoyape, 8 (CNHM); Cabache, 1 (CNHM). *Amazonas:* Chachapoyas, 13 including type of *stenops* (CNHM, 10; AMNH, 3); San Pedro, south of Chachapoyas, 6 (CNHM); Tambo Carrizal, the type of *tamborum* (CNHM). *Cajamarca,* 10 (AMNH, 1; CNHM, 9); Hacienda Limón, 2 (CNHM). *La Libertad:* Hacienda Llagueda, 2 (CNHM); mountains near Otuzco, 2 (CNHM). *Ancash:* Macate, 41 (AMNH, 2; CNHM, 36; USNM, 3); Yungay, 11 (CNHM); Huaras, 14 (CNHM); Quebrada Quilcayhuanca, Huaras, 11 (CNHM); Hacienda Catac, Ticapampa, 8 (CNHM). *Huánuco:* Cullcui, 3 (CNHM); Ambo, 10 (AMNH, 1; CNHM, 8; USNM, 1). *Lima:* Matucana, 7 (CNHM, 3; MVZ, 4); Surco, 3 (CNHM, 1; MVZ, 2); Casapalca, 4 (MVZ); Canta, 1 mile west, 2 (MVZ); Huarós, 8 (MVZ); San Mateo, 6 (MVZ); Villavista, 8 (MVZ); Zarate, 10 (MVZ); San Bartolomé Station, 1 (MVZ).

Phyllotis darwini Waterhouse. (Synonymy under the species and subspecies.)

Distribution (figs. 57, 70).—From the departments of Junín, central Peru, south along the Pacific coast and highlands through Peru, Chile, Bolivia and Argentina to the Straits of Magellan, and east to the Atlantic coast in the Argentine departments of Santa Cruz and Comodoro Rivadavia; altitudinal range from sea level to 5000 meters above or to snow line.

Characters.—External, cranial and dental characters are those of the *P. darwini* group; base of baculum convex or nearly plane as described elsewhere (p. 58, figs. 5–8).

Comparisons.—*Phyllotis darwini* figures in comparisons made between members of the *darwini* complex, with other species of the genus *Phyllotis* (p. 236) and with phyllotines in general. The geographic relationship between *P. darwini* and other members of the complex is discussed under the heading Sympatry and Allopatry (p. 31). Differences between *P. darwini* and sympatric representatives of *P. osilae* are shown in Tables 30–49, and pp. 346–357. The differences are idealized in figure 86. Comparisons between *P. darwini* and sympatric series of *P. andium* are made in the account of the latter.

Variation.—GEOGRAPHIC: The ten subspecies of *P. darwini* recognized here are, from north to south, *definitus, posticalis, limatus, rupestris, magister, wolffsohni, caprinus, darwini, fulvescens* and *xanthopygus.* The palest race, *Phyllotis darwini rupestris* and *P. d. limatus* live in the driest parts of the range of the species; the most saturate race, *fulvescens,* inhabits areas of high rainfall. The finely graduated increase in humidity along the Pacific Coast from southern Peru to southern Chile is correlated with a correspondingly fine transition from *limatus* and *rupestris,* through more intensely colored *darwini,* to saturate *fulvescens.* The boundaries of the ranges of most subspecies conform closely to the hyetal lines which demarcate the principal zones of rainfall. There is no such correlation between altitude *per se* and color or any other subspecific character.

A size gradient between subspecies is not apparent. *P. d. rupestris* averages smallest but intergrades directly or indirectly with all other races. *P. d. rupestris* becomes larger from western Peru and Chile eastward into the high Andes but without significant differentiation in proportions or other characters. This even gradient is no basis for divisions into the two or more subspecies (*chilensis, vaccarum, ricardulus*) recognized by other authors. On the other hand where the change in size is abrupt as in the case of *rupestris* and *magister* no cline is evident but two sharply defined taxons are.

Tail length averages slightly less than combined head and body length in present samples of *rupestris, darwini* and *xanthopygus*, slightly more than head and body length in *posticalis, wolffsohni* and *magister*, considerably more in *limatus* (118:100), and most in *caprinus* (122:100). It is significant, however, that practically the full specific range of variation of tail length relative to head and body length obtains in such races as *P. d. posticalis* (72–137:100) and *rupestris* (81–132:100). More specimens of these than of other races were examined.

The principal obliquity in cranial characters is the strongly divergent-sided supraorbital region in most specimens of *wolffsohni*. The same race is also noteworthy for the consistent S-shaped pattern of its second molars and, to a slightly lesser extent, of its third upper molars. *Phyllotis darwini caprinus* bridges the gap between *wolffsohni* and other races of *darwini* (figs. 82–84).

LOCAL: Size differences between two neighboring micropopulations, or pocket populations, of a subspecies may be greater than the average size difference between two neighboring subspecies. The tail may average considerably longer than combined head and body length in some local concentrations of individuals and considerably shorter in others. For example, in the 5 specimens of *P. darwini posticalis* from San Jenaro, Santa Inez, Huancavelica, the ratio of the tail to head and body is 83, 85, 86, 86, 86, respectively; in the 4 specimens of *posticalis* from Urco, Cusco, the tail ratio is 117, 121, 126, 136, respectively. A group of individuals inhabiting a comparatively humid pocket of an otherwise generally dry region may be slightly darker than average in coloration. Pelage of populations inhabiting warm coastal areas may be shorter, thinner, and coarser in texture than that of populations of the same race living near the border of perpetual snow. Local differences in the chemical composition of solubles in drinking water may cause striking local differences in bulk and density of cheek teeth. These and similar gross deviations from the overall racial pattern may be impressive when subjected to statistical analysis. For the most part, however, they are reflections of age, crop and random genetic variations.

INDIVIDUAL AND AGE: The classical concept of the existence of a direct relationship between the age of an individual and its size, pelage, and dental conditions can be applied with some degree of confidence only to individuals of the same crop. It cannot be applied generally to phyllotine rodents or, for that matter, to any mammal without qualifications which are frequently nullifying. Pel-

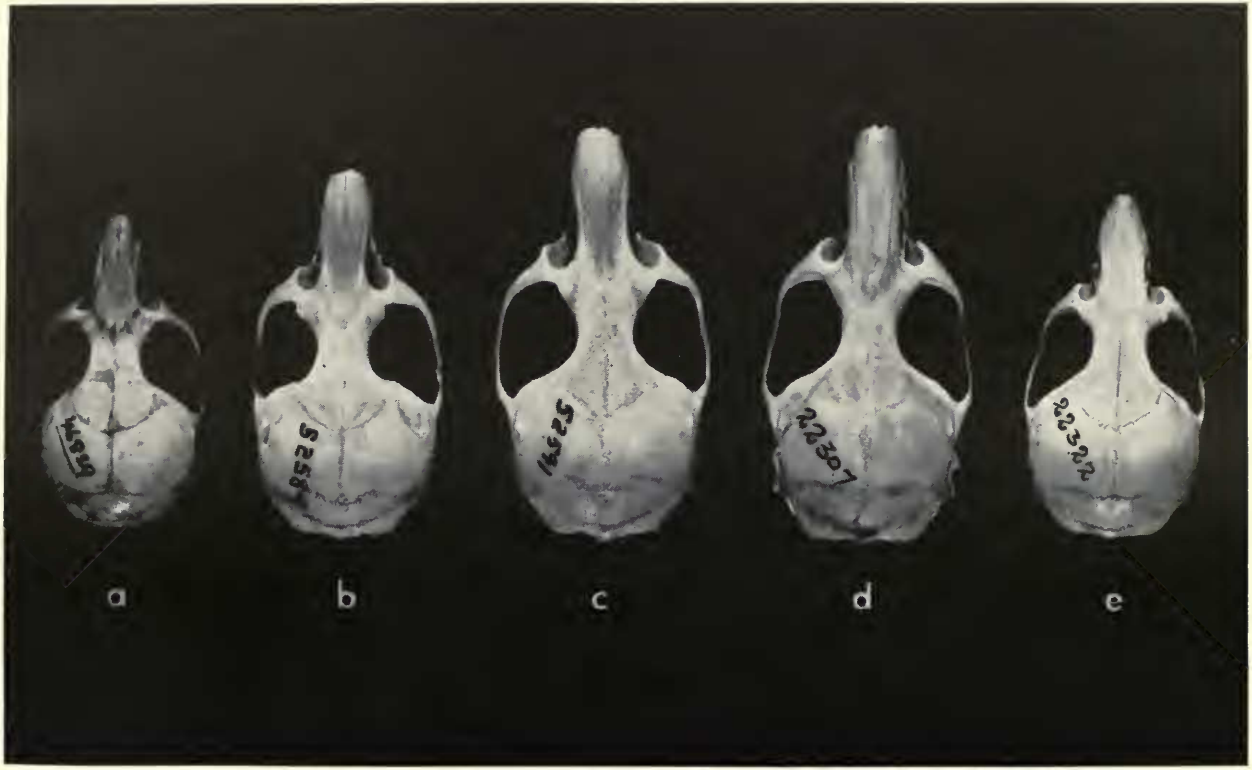
a
b
c
d
e
5258
52591
22307
22322

FIG. 78.—Dorsal aspect of skulls of *a*, *Phyllotis haggardi* and *b–e*, *P. darwini rupestris*, showing variation in size. (About ×1¾).

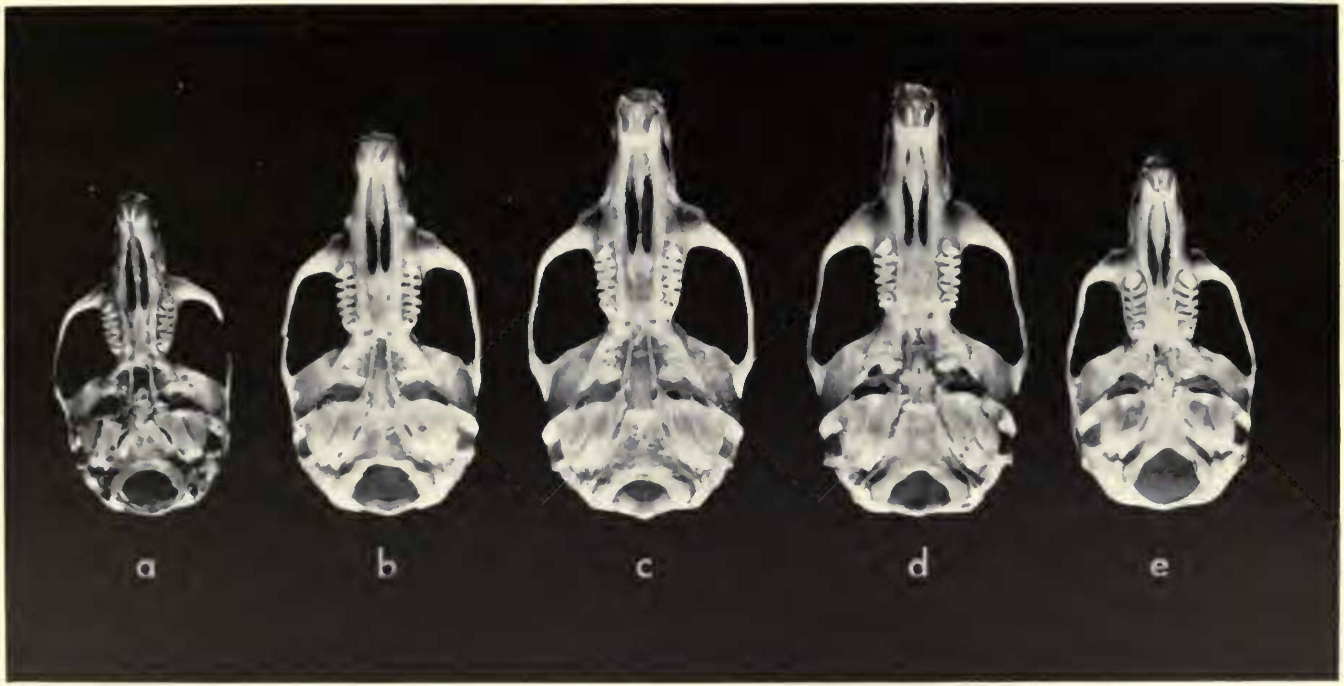

FIG. 79.—Palatal aspect of same skulls shown in figure 78.

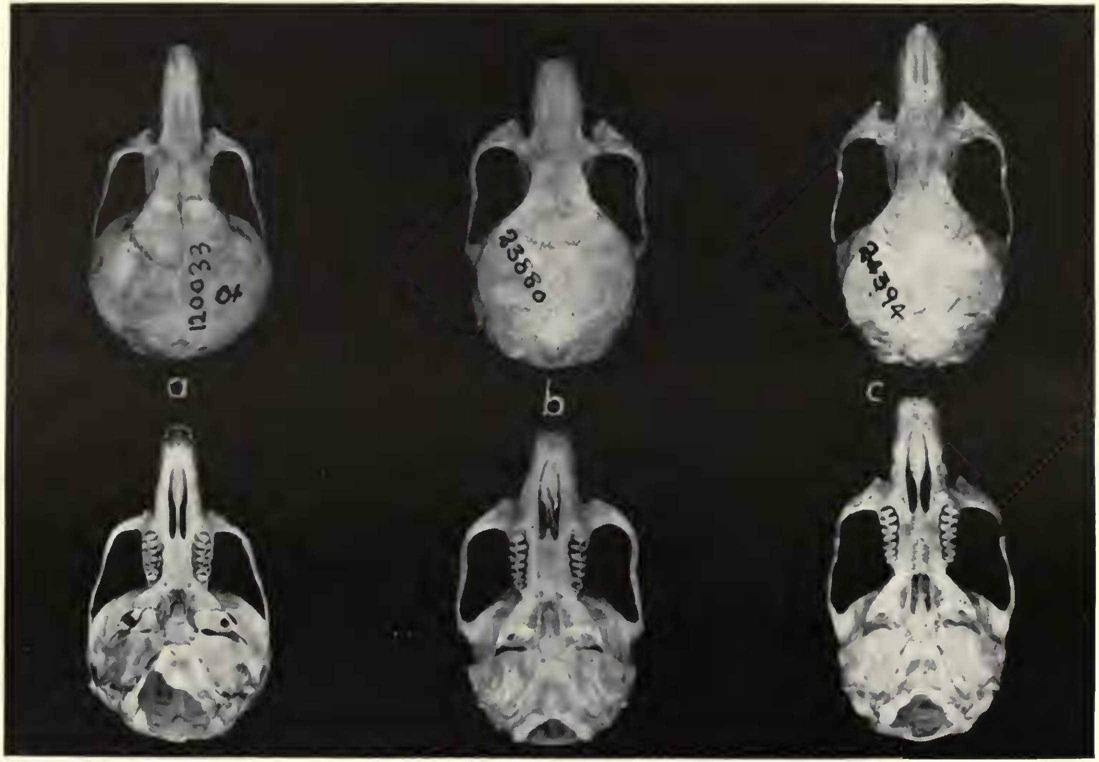

FIG. 80.—Abnormal skulls of *Phyllotis darwini*; *a*, hydrocephalic skull of *P. d. limatus* from Surco, Lima, Peru; *b*, abnormal skull of *P. d. darwini* from Valparaiso, Chile; *d*, normal skull of *P. d. darwini* from Valparaiso, Chile. (About × 1½.)

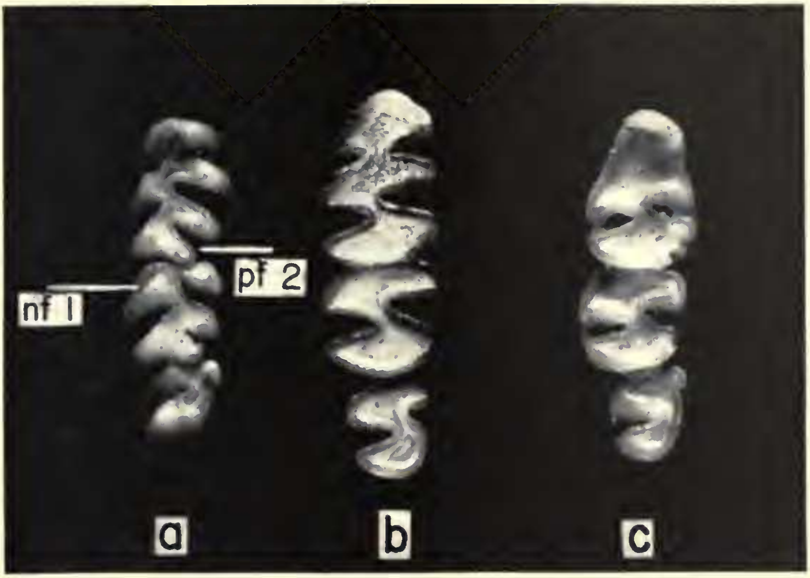

FIG. 81.—Left lower molar of *Phyllotis darwini:* *a*, unworn; *b*, moderately worn; *c*, well worn.

ages of independently active juvenals and older individuals are, as a rule, practically indistinguishable. The last molar of independently active juvenals is as fully developed and functional and may even be as worn as in adults (figs. 81, 82). Dry season generations or crops of mice may be smaller individually and collectively and even paler, than their rainy season counterparts. Molars of dry season crops of mice may show considerably more abrasion than those of an older, rainy season crop. Change of pelage, or molt, among adults is individually variable. Dominance of one pelage phase over another may be suspected in a given series, or for a given season, but all adults of a population do not undergo the same stages of molt at the same time. Extraordinary differences in size, condition of pelage and molar attrition may exist among individuals reared in highly specialized or artificial habitats and their contemporaries occupying the natural habitats of the same region.

SEXUAL: In all series with a goodly number of adults of both sexes, males average slightly larger than females.

Habits and habitat.—*Phyllotis darwini* is the ubiquitous cricetine of the southern Andean countries. This terrestrial and scansorial rodent abounds in deserts, scrublands and temperate zone grasslands, but appears to be scarce, if not merely an occasionally intrusive element, in primary forest. Erstwhile wooded areas of Peru, Bolivia and Argentina had already been cleared by man in localities where specimens of *P. darwini* were collected. On the other hand, the type of *P. d. fulvescens* was discovered in the Araucaria forest of the Cordillera de Nahuelbuta, southern Chile. When describing *fulvescens*, Osgood (1943, p. 204) remarked that "in a week's intensive collecting, with three lines of traps out, only the single specimen (the type) was obtained and this not in a mouse trap, but in a steel trap set at the burrow of *Aconaemys*." About the same time, H. E. Anthony secured another specimen, farther north in the same region. The Araucaria forest is abundantly gladed and cannot be more than an ineffective barrier to savanna animals. Except for the tiny marsupial *Marmosa pusilla*, this region, like all Chile, has no arboreal mammalian fauna. According to Darwin (*in* Waterhouse, 1839, p. 65) the species bearing his name "inhabits dry stony places," in the vicinity of Coquimbo, Chile. On the other hand, the original specimens of *P. d. xanthopygus* taken by Darwin (op. cit., p. 64) are "extremely abundant in the coarse grass and thickets in the ravines at Port Desire and Santa Cruz" in southeastern Argentina. Emilio Budín (*in* Thomas, 1919b, p. 200) secured specimens of *xanthopygus* "among the cactus plants" in western Argentina.

Pearson (1951, pp. 142, 144) described *P. darwini* of the Peruvian altiplano as "a mouse of rocky places. Boulders, rock slides, cliffs, small shale outcroppings, stone walls, and stone huts are all satisfactory habitations. . . . All the specimens were caught at night, many of them in the first hour of darkness. Several wild caught individuals had green vegetable pulp in their stomachs, but a caged specimen ate assorted grains and ignored the tola bush (*Senecio adehophylloides*) which its cagemate, a *Punomys*, relished." Regarding sympatry with *Phyllotis osilae*, Pearson (1958, p. 399) observed that "the two species may be taken on the same trap line, but the *osilae* are usually among the bunch grass locally called *ichu* (usually *Stipa ichu*) and the *darwini* in more open rocky places near by. The same habitat preferences extend from southern Peru south at least to Jujuy in northern Argentina, which is as far south as I have collected, and the sympatry exists between several subspecies pairs: [*Phyllotis*] *osilae osilae* and [*P.*] *darwini posticalis* near Cuzco, *osilae phaeus* and *darwini posticalis* near Limbani in southern Peru, *osilae osilae* and *darwini chilensis* [=*rupestris*] in the Titicaca Basin, *osilae osilae* and *darwini rupestris* in Bolivia, and *osilae tucumanus* and *darwini ricardulus* in Catamarca

. . . . Dr. Karl Koford states in his field notes that 5 *osilae* taken above Limbani were trapped in thick grass, and that most of the 18 *darwini* that he collected there were trapped in rocky areas."

Refuge and nesting site of the leaf-eared mouse may be in a burrow of its own or in that of another animal. The Argentine collector, Budín (*in* Thomas, 1926b, p. 604), caught specimens of *Phyllotis darwini* and *Cavia* sp. in traps set at the mouth of cavy burrows, and believes the two rodents live together. The Chilean naturalist, John Wolffsohn, addressed a letter to Oldfield Thomas (1927, p. 556) with the statement that he found *Phyllotis darwini* in the same holes with *Octodon degus, O. bridgesi, Abrocoma bennetti, Akodon olivaceus, Abrothrix longipilis, Oryzomys longicaudatus, Rattus rattus,* and *Marmosa elegans.* This unprejudiced rodent also makes itself at home in man's dwellings and other structures where (*fide* Mann, 1945, p. 40) it competes successfully with the Old World house rat, *Rattus rattus*).

Accounts of *ratadas,* or periodic concentrations of great numbers of mice in localized areas where certain foods are available, do not refer specifically to any *Phyllotis.* It is reasonable to assume, however, that the omission reflects the poor state of knowledge of the systematics of cricetines. No doubt *P. darwini,* by virtue of its wide distribution, local abundance, and aggressive instincts, plays a frequent and prominent role in *ratadas.*

Reproduction.—Breeding habits of *Phyllotis darwini* observed by Pearson (1951, p. 143) during 1946 in the department of Puno, Peru, have been recorded as follows: "Males and females at Pairumani [Puno, Peru, 4060 meters altitude] were not in breeding condition from July 17 to 21 [1946], yet several males at Santa Rosa [same region, 4375 meters] from July 23 to 25 [1946] had testes 9 to 10 mm. long. Pregnant females were caught at Santa Rosa on July 28 and August 1, but at Caccachara [same region, 5000 meters] none were caught until October 5 [1946]. Pregnant females and breeding males were caught frequently between this date and December 19, and immature specimens were caught on December 9. The average number of embryos was 4. In all 6 cases where the necessary data were recorded, there were more embryos in the right horn than in the left. The ratio of sexes was 64 males to 44 females."

Additional breeding data collected in 1951, 1952 and 1955 by Pearson and associates and noted on the skin tags of specimens are tabulated below (Table 15).

TABLE 15.—Reproduction in *Phyllotis darwini;* summary of manuscript data on skin tags of specimens collected by O. P. and A. K. Pearson, C. B. and M. Koford, and E. Heller.

(See page 242 for locality data and page 281 for explanation of symbols.)

Month	Locality[1]	♀♀[2]	♂♂[3]	Subspecies
January	Tarata, Tacna	0,0,0,0,0	11,11,11,11,12,13	*magister*[4]
	Tarata, Tacna, 11,500–12,200 ft.	J,2,J5,5	8,9,10	*rupestris*[4]
	Tarata, Tacna, 12,800–15,200 ft.	J,0,0,0,3,J4	9.5,10,10,11,11,11.5,12	,,
	Lago Suche, Moquegua	J,0	11	,,
	Torata, Moquegua	J	9	,,
	Ilave, Puno	J	12,12	,,
	Juli, Puno	J,0,0	5	,,
	Pomata, Puno	0	11	,,
February	Ancomarca, Puno	0	11,11	*rupestris*
	Puno, 15 km. W, Puno	J		,,
	Puno, 82 km. W, Puno	0	11.5	,,
	Pairumani, Puno	4	13	,,
March	Atico, Arequipa		6,14	*limatus*
April	Santa Rosa, Puno		10,12	*rupestris*
May	Atico, Arequipa	0	6	*limatus*
	Chucarapí, Arequipa	0	3	,,
	Arequipa, Arequipa	0		*magister*
	Chihuata, Arequipa	L,L	13	,,
	Mt. Misti, Arequipa	0		,,
	Puquio, Ayacucho	3	12,12	*posticalis*
	Limbani, Puno	O,L	J5,12,13	,,

TABLE 15.—Reproduction in *Phyllotis darwini*; summary of manuscript data on skin tags of specimens collected by O. P. and A. K. Pearson, C. B. and M. Koford, and E. Heller (*continued*).

Month	Locality[1]	♀♀[2]	♂♂[3]	Subspecies
June	Umayo, Puno	0	4,3,7	*rupestris*
	Arapa, Puno	0		,,
	Limbani, Puno	J,0	8,12	*posticalis*
July	San Pedro, Atacama[5]	0	4	*rupestris*
	Limbani, Puno	0,L		*posticalis*
August	Mazocruz, Puno	0		*rupestris*
	Juliaca, Puno		11	,,
	Tarata, Tacna		4,9	,,
	Santa Eulalia, Lima	J,4	J2,9,10	*limatus*
	Naña, Lima		5,9	,,
	Chosica, Lima	0,0,L,L,P	7,9,10,11	,,
	Rimac Valley, Lima	3,4	J6,9,12	,,
	S. Bartolomé, Lima	J,J,L	8	,,
	Surco, Lima	0		,,
	Ayacucho, Ayacucho	0	4,5	*posticalis*
	Río Mantaro, Huancavelica	0,0		,,
	Limbani, Puno	0,0	4	,,
September	Tilcara, Jujuy[6]	0,0,0,0	7,10,11,11	*caprinus*[7]
	Yuruma, Potosí[8]		3	,,
	Tapacari, Cochabamba[8]	0,0,0	4,4,5,6	*wolffsohni*

TABLE 15.—Reproduction in *Phyllotis darwini;* summary of manuscript data on skin tags of specimens collected by O. P. and A. K. Pearson, C. B. and M. Koford, and E. Heller (*continued*).

Month	Locality[1]	♀♀[2]	♂♂[3]	Subspecies
	Punata, Cochabamba[8]	0,0,0	4,4	*wolffsohni*
	Comarapa, Santa Cruz[8]	0	3,5,6,6	"
	Caritaya, Tarapacá[5]	0,0	9,10,10,10	*rupestris*
	Tilcara, Jujuy[6]	0,0,0,0	5,6,6	" [7]
	La Paz, La Paz[8]	0	10,10,10	"
	Oruro, Oruro[8]	0	3	"
	Uyuni, Potosí[8]	0,0	4,J6,8,9,9,9,10,10	"
	Villazón, Potosí[8]	0	5	"
	Limbani, Puno	0,0	12	*posticalis*
October	Camataquí, Tarijá[8]	0	4,4,4,5	*rupestris*
	Villazón, Potosí[8]	0,0,0	5	"
	Potosí, Potosí[8]	0,0,0,0	4,4	"
	Toconce, Antofagasta[5]	4	8,10	"
	Tatio Geysers, Antofagasta[5]		8	"
	San Pedro, Atacama[5]	0	10	"
	Tarata, Tacna		7,9	"
	Tarija, Tarija[8]		5	*caprinus*
	Camataquí, Tarija[8]	0,0,0,0,0,0,0,0	t,t,s,s,4,4,4,4,4,4,4,5,7	"
	Camargo, Chuquisaca[8]	0	6,7	"
	Limbani, Puno		9	*posticalis*
November	Huaylarco, Arequipa	3,7	11,11	*rupestris*
	Tincopalca, Puno		11	"
	Puno, Puno	2	6	"
	Asillo, Puno		11	"

TABLE 15. Reproduction in *Phyllotis darwini;* summary of manuscript data on skin tags of specimens collected by O. P. and A. K. Pearson, C B. and M. Koford, and E. Heller (*concluded*).

Month	Locality[1]	♀♀[2]	♂♂[3]	Subspecies
December	Torata, Moquegua	0,0	8	*magister*
	Arequipa, Arequipa	0,L	7,8,9,9.5,10	*rupestris*
	Arequipa, 12 km. SSW, Arequipa	J2	9,10,10	,,
	Salinas, Arequipa		7,10	,,
	Imata, Arequipa		12	,,
	Torata, Moquegua		7.5,8,8,8.5,9,10	,,
	Lago Suche, Moquegua		12	,,
	Tala, Moquegua	0,5		,,
	Caccachara, Puno	0		,,
	Puno, Puno	3	10,11,12	,,
	Río Santa Rosa, Puno		10,10,11	,,

[1] All localities in Peru unless otherwise indicated.

[2] Each number (0–7) represents the number of embryos in each female.
J = virgin or young.
L = lactating.
P = vaginal plug present.

[3] Each number (4–14) represents length of testes in millimeters in each male.
J = juvenal.
s = "small" testes.
t = "tiny" testes.

[4] Tarata *magister* and Tarata *rupestris* are sympatric (cf. p. 290).

[5] Chile.

[6] Argentina.

[7] Tilcara *caprinus* and Tilcara *rupestris* are ecologically segregated (cf. p. 335).

[8] Bolivia.

The data may be summarized as follows:

1. Highest proportions of gravid and suckling females occur from November to February and in August.

2. Most males are in breeding condition from November to May.

3. Lowest proportions of gravid and suckling females occur during September and October.

4. Most non-breeding males occur from July to October.

5. Means and extremes of the number of embryos are 4.6 (2–7) 12 females.

6. Sexual maturity is attained at a stage of external, cranial and dental development which would be classified as subadult or juvenal.

7. The annual breeding cycles and reproduction in *Phyllotis darwini* correspond roughly to those of *Phyllotis osilae* for which comparable data are available (p. 351, Table 29) and agree with the generalized observations on altiplano cricetines made by Dorst (1958, p. 563).

8. The existence of a local and/or regional breeding cycle or cycles may be suggested but is not established by available data. Present information is derived from kill-trapped individuals taken during one or two successive trapping nights per locality. Such samples do not necessarily reflect the true breeding condition of the population at any moment or month or even a fair approximation of the ratio of individuals belonging to each sex and age class.

Phyllotis darwini posticalis Thomas

Phyllotis darwini posticalis Thomas, 1912, Ann. Mag. Nat. Hist., (8), **10**: 406. Thomas, 1920, Proc. U. S. Nat. Mus., **58**: 230—part, *Cusco* (Huaracondo [part]; Chospioc; Ollantaytambo [part]; Puquiura[?]). Pearson, 1958, Univ. California Publ. Zool., **56**: 414—characters; distribution (see p. 242 for locality records); *abrocodon* Thomas a synonym.

P[*hyllotis*] *d*[*arwini*] *posticalis*, Osgood, 1915, Field Mus. Nat. Hist., Zool. Ser., **10**: 190, footnote—*Junín* (Oroya).

[*Phyllotis darwini*] *posticalis*, Osgood, 1944, Field Mus. Nat. Hist., Zool. Ser., **29**: 194—possibly recognizable as a subspecies; *abrocodon* Thomas a synonym.

Phyllotis abrocodon Thomas, 1926, Ann. Mag. Nat. Hist., (9), **17**: 316—PERU: *Junín* (type locality, La Oroya, Lake Junín, 3750 meters).

Type.—Adult female, skin and skull, British Museum (Natural History) no. 0.7.7.38; collected by Perry O. Simons, 26 February, 1900.

Type locality.—Galera, a railway station on the crest of the Cordillera Occidental, Yauli Province, department of Junín, near boundary of Lima Department, Peru; altitude, 4800 meters above sea level.

Distribution (figs. 70, 72, 73, 76).—Andes of Peru from northern Junín and bordering parts of Lima southward into Huancavelica, Ayacucho, Apurimac, Cusco and the upper Río Inambari basin in Puno; altitudinal range approximately 1900 to 5000 meters above sea level.

Characters.—Average size slightly less than *definitus* and *magister*, larger than *limatus* and *rupestris;* paler than *definitus* and sympatric populations of *Phyllotis osilae* but darker, more gray, than average *magister, rupestris* and *limatus;* dorsal surface pale brown finely peppered with black, giving a dark grizzled effect; side of head, rostrum, and shoulders usually more gray than trunk; well-defined gray underparts with a light, sometimes a moderate, wash of buff or ochraceous; pectoral streak or patch present or absent; tail usually longer than combined head and body length, thinly haired or well-haired, bicolor except sometimes at tip, rarely nearly entirely dark brown; ratio of tail to combined head and body length=70–137: 100; auditory bullae moderately inflated; average antero-posterior length, less tubes, about 4.8 mm. (4.4—5.4, 95 specimens) and always less than alveolar length of molar row; mesopterygoid fossa comparatively broad, the anterior border usually square or slightly rounded, rarely pointed as in *definitus;* posteromedian process of palate little developed or absent; posterolateral palatal pits usually anteriad to posterior border of palate but may be on a line with or posteriad; supraorbital edges sharp or rounded, the edges often raised to form a well-defined though shallow frontal sulcus, proximal ends of nasals pointed to truncate and terminating from in front of to behind fronto-premaxillary sutures; molars moderate to large, combined alveolar length, in adults, 4.9–6.1 mm. (99 specimens) or 17–19 per cent of greatest skull length.

Variation.—Smallest members of the race occur at the southern extreme of the range, in Cusco, where contact with equally small *Phyllotis osilae* occurs, and at the northern extreme, in Junín and Lima, where similarly sized *P. andium* lives. Populations of large *posticalis* including some quite like *Phyllotis darwini magister,* occur in the central and southwestern parts of the range in the departments of Huancavelica, Ayacucho and Apurimac.

Size of molars as measured by their alveolar lengths varies in adults from 17 to 19 per cent of greatest skull length. The narrow range in proportional length indicates that longer molar, or alveolar, rows, are associated with larger skulls, smaller rows with smaller skulls and that the length of the row increases with cranial growth until old age when molar attrition is greater. In a series of 5 specimens from Hacienda Palmira, Apurimac, the largest skull, with length 33.0 mm., has the largest molars, with an alveolar row length of 6.0 mm. The second smallest fully adult skull, with length 30.6, has the smallest molars, with an alveolar row length of 5.5. The smallest adult skull (30.1 mm.) has an alveolar row of 5.6. The ratio of alveolar row to skull length is approximately 18 per cent in each of the five specimens of the series. The largest set of molars in the Palmira series is the least worn, the smallest the most worn.

Palest populations of *posticalis* are in Cusco (Cusco; Sacsahuaman). They grade into pale *rupestris* of Arequipa and Puno. Others from Cusco (Ccolini) and Puno (Limbani) are virtually indistinguishable from extremely dark Bolivian representatives of *Phyllotis osilae.* More typically colored *posticalis* from Ayacucho, Apurimac and Huancavelica are like the darker series of *magister* from Chihuata, Arequipa. Northward, in Junín, *posticalis* is more brown, and distinction from neighboring *Phyllotis andium* is based on characters other than color. Nowhere, however, does *posticalis* become as warmly brown as *P. darwini definitus.* In general, pale populations occur in drier areas, dark populations in more humid regions.

The tail is generally bicolor except sometimes for a brownish tip. A single specimen from Ccolini, Marcapata, Cusco, collected 27 August, 1953, is unusually dark with terminal two thirds of tail uniformly brown.

Hairiness of tail varies locally to a marked degree. In the departments of Lima, Junín and Puno, tails are generally hairy with well-developed pencils. In Huancavelica, Apurimac and Ayacucho, the tails of some populations are quite hairy while those of others are thinly haired with virtually no pencil. In still others, tails range from thin to thickly haired.

A buffy or brownish pectoral streak or patch is frequently present and often correlated with dark underparts and a thinly haired tail as in *Phyllotis osilae.* Cranial characters common to *P. osilae* may also be associated with the *osilae*-like external characters. Specimens of *posticalis* from several localities in Huancavelica (Piso;

Lircay; Palmira) are like *P. osilae* and except for their *darwini* type penis bones could be so classified. In some Cusco localities (Huaracondo; Ollantaytambo; Urco) and Puno (Limbani) where *posticalis* and *P. osilae* occur, the former is more typically *darwini* in external and cranial characters.

The front of the upper incisors is white with an orange mottling in two of five specimens from Palmira, Apurimac. This character served as the basis for the description of *Phyllotis abrocodon* Thomas from La Oroya, Junín. The incisors are normally pigmented orange in two specimens at hand which formed part of the original *abrocodon* series of twelve examined by Thomas.

Pink-stained skulls in *posticalis* have been noted by Pearson (1958, p. 415). He suggested that the stain may have been derived from ingested cochineal. I tested the theory by feeding cochineal to laboratory mice (*Mus musculus*). Their bones stained the same as in the *Phyllotis*. The pink skulls of *P. darwini posticalis* in Chicago Natural History Museum and the University of California Museum of Vertebrate Zoology (MVZ) are listed as follows:

Catalog Number	Locality	Date of Collection
20917	La Oroya, Junín	28 June, 1925
75421	Puente Pajonal, Ayacucho	22 October, 1953
75422	Puente Pajonal, Ayacucho	22 October, 1953
75423	Puente Pajonal, Ayacucho	23 October, 1953
75424	Puente Pajonal, Ayacucho	23 October, 1953
120004 (MVZ)	Ayacucho, Ayacucho	30 August, 1955
75425	Piso, Huancavelica	8 December, 1953
75426	Piso, Huancavelica	8 December, 1953
75436	Mayoc, Huancavelica	5 December, 1953
75439	Mayoc, Huancavelica	4 December, 1953
75440	Mayoc, Huancavelica	5 December, 1953
120006 (MVZ)	Río Mantaro, Huancavelica	29 August, 1955
120007 (MVZ)	Río Mantaro, Huancavelica	29 August, 1955

There are two more skulls from La Oroya, and two from Ayacucho, all unstained. Two skulls of *Calomys sorellus* from Puente Pajonal, collected at the same time as the *Phyllotis*, are similarly stained pink.

Taxonomy.—Phyllotis darwini posticalis combines in one or another of its populations all external, cranial and dental characters of the forms originally described as *Phyllotis andium*, *P. osilae*, *P. magister* and *P. definitus*. Absolute distinction of *posticalis* and *P. osilae* depends solely on slight and dubiously constant differences in the structure of the penis (fig. 7). The same may be true of *P.*

TABLE 16.—Measurements of *Phyllotis darwini posticalis* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
Carhuamayo	135(126–148)8	129(122–135)8[1]	29.6(28–31)8	—	30.9(29.7–32.9)7	16.3(15.7–16.9)7	5.7(5.4–6.0)8
Oroya[2]	122	137	28	26.5	31.5	16.3	5.2
Oroya	109	—	27	—	31.0	15.3	5.6
Galera[3]	117	122	25	27	30.7	—	5.3
Junín	118,120	120,130	28,29	—,—	30.5,31.2	15.6,16.0	5.5,5.6
Casapalca	116(102–120)9	119(110–127)9[4]	27(26–28)9	25(24–28)9	30.6(29.7–32.0)9	15.7(15.2–16.2)9	5.6(5.4–5.8)9
Mayoc	123,136	135,142	29,30	27,27	31.3,33.6	16.4,16.9	6.0,6.0
Mantaro	121	128	27	25	30.0	15.6	5.9
Piso	131,137	137,139	30,29	26,27	31.5,33.0	15.9,16.8	5.5,5.7
Huancavelica	131(118–141)16	130(118–145)15[5]	29.4(28–31)16	26.6(25–28)16	31.5(29.7–33.7)14	16.2(15.2–17)14	5.7(5.2–6.1)14
Lircay	130,130,139,143	140,130,146,137	31,30,30,30	27,28,26,28	31.3,31.8,32.5,32.5	15.3,15.9,16.5,16.5	6.1,6.1,5.9,6.0
San Jenaro	130,138,133,132	112,117,110,113	28,28,29,28	26,26,25,26	30.6,31.1,31.4,31.6	15.2,15.5,15.9,15.6	5.4,5.4,5.6,5.4
Pajonal	130,148,145,145	145,142,140,165	30,30,32,32	26,26,27,25	31.9,32.3,34.3,34.6	16.9,16.5,17.6,17.5	5.9,5.8,6.1,6.1
Polanco	129	132	27	25	31.1	16.3	5.2
Ayacucho	110,113	139,135	29,29	24,24	30.8,30.8	15.6,16.2	5.7,5.7
Palmira	131(115–153)5	132(120–146)4[6]	29(28–30)5	26.6(25–28)5	31.5(30.6–33.0)5	16.4(16.0–16.7)5	5.8(5.5–6.0)5
Puquio	113,128,134	110,—,138	25,28,28	24,27,26	30.6,33.2,33.2	15.8,16.6,17.1	5.4,5.6,5.9
Urco[7]	111,103,104	130,125	27,27	24,23,25	28.7,28.8,29.8	15.1,14.4,14.7	5.4,5.1,5.4
Sacsahuaman	110(101–125)5	122(109–140)5[8]	27(26–28)5	23.6(23-25)5	28.8(27.5–31.0)5	15.3(14.7–15.9)5	5.2(4.9–5.4)5
Cusco	130,130,128,141	127,143,121,129	31,30,30,30	—,—,—,—	30.1,30.5,30.6,32.6	15.2,15.6,15.9,16.4	5.2,5.1,5.3,5.7
Macchu Picchu	120	125	27	22	29.9	—	5.7
Ollantaytambo[7]	130	137	29	24	32.6	16.2	5.7

TABLE 16.—Measurements of *Phyllotis darwini posticalis* Thomas (*continued*)

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
Chospioc	128	146	28	25	31.4	16.1	—
Huaracondo[7]	125	142	28	26	34(c)	—	5.3
Ccolini	138	140	29	27	33.6	17.0	5.9
Perayoc	117	137	29	24	29.8	15.9	5.5
Calca	123	133	29	24	—	—	5.8
Pisac	132,134	144,143	30,31	25,25	31.8,31.6	16.3,15.5	5.5,5.8
Limbani 13,000 ft.[7] [9]	110,123	130,140	28,29	29,26	29.4,30.2	15.5,15.5	5.1,5.3
Limbani, 15,000 ft.[10]	121(112–131)14	126(115–144)14[11]	28(26–30)14	29(26–31)13	31.2(29.3–32.9)12	16.2(15.6–17.1)12	5.3(4.9–5.7)13

[1] Tail of 1 longer, of 7 shorter than combined head and body length. Tail: head and body=(90–103):100.

[2] Type of *abrocodon*, measurements from original description.

[3] Type of *posticalis*, measurements from original description.

[4] Tails of 5 longer, of 2 equal, of 2 shorter than combined head and body length. Tail: head and body=(93–112):100.

[5] Tails of 10 longer, of 4 shorter, than combined head and body length, and 1 of equal length. Tail: head and body=(92–103):100.

[6] Tails of 3 longer, of 1 shorter, than combined head and body length. Tail: head and body=(94–113):100.

[7] See Table 45, p. 374, for additional data and comparisons with sympatric samples of *Phyllotis osilae*.

[8] Tails of all longer than combined head and body length. Tail: head and body=(101–123):100.

[9] Weights, in grams, 41, 50, respectively.

[10] Weights, in grams, 54 (38–75) 14.

[11] Tails of 8 longer, of 6 shorter than combined head and body length. Tail: head and body=(89–115):100.

andium. P. definitus grades into *posticalis* while *magister* is virtually indistinguishable. The variability, plasticity and geographic position of *posticalis* are such that all species of the *darwini* group can be derived from it.

Measurements.—See Table 16 (p. 286).

Specimens examined.—118. PERU.—*Apurimac:* Hacienda Palmira, 5 (CNHM). *Ayacucho:* Ayacucho, 2 miles south, 3 (MVZ); Puente Pajonal, Ocros, 4 (CNHM); Puquio, 35 km. ENE, 2 (MVZ); Puquio, 15 km. NE, 1 (MVZ); Tambo, Polanco, 1 (CNHM). *Cusco:* Ampay, 3 (CNHM); Ccolini, Marcapata, 1 (CNHM); Chospioc, 5 (USNM); Cusco, 4 (CNHM); Fundo Perayoc, 1 (CNHM); Hacienda Ccapana, Ocongate, 1 (CNHM); Hacienda Paullo Grande, Calca, 2 (CNHM); Hacienda Urco, 4 (CNHM); Huaracondo, 1 (USNM); Ollantaytambo, 1 (USNM); Sacsahuaman, 5 (CNHM). *Huancavelica:* Hacienda Piso, Locroja, 2 (CNHM); Huancavelica, 16 (CNHM); Lircay, 4 (CNHM); Mayoc, 3 (CNHM); Río Mantaro, 2 (MVZ); San Jenaro, Santa Inés, 5 (CNHM). *Junín:* Carhuamayo, 8 (CNHM); Junín, 2 (CNHM); La Oroya, 3 (CNHM). *Lima:* Casapalca, 11 (MVZ). *Puno:* Limbani, 8 miles SSW, 16 (MVZ); Limbani, 4 miles SSW, 2 (MVZ).

Phyllotis darwini magister Thomas

Phyllotis magister Thomas, 1912, Ann. Mag. Nat. Hist., (8), **10**: 406. Pearson, 1958, Univ. California Publ. Zool., **56**, (4): 429—characters.

Phyllotis magister magister, Pearson, 1958, Univ. California Publ. Zool., **56**, (4): 430—PERU: *Arequipa* (Arequipa; Chihuata, 2 miles east; Mt. Misti; Tingo; Yura); *Moquegua* (Río Torata); *Tacna* (Tarata); taxonomy.

[?] [*Phyllotis darwini*] *limatus*, Thomas (part, not Thomas), 1920, Proc. U. S. Nat. Mus., **58**: 230—PERU: *Arequipa* (Arequipa).

Type.—Male, skin and skull, British Museum (Natural History) no. 0.10.1.31; collected 29 March, 1900, by Perry O. Simons.

Type locality.—Arequipa, Arequipa, Peru; altitude, 2300 meters.

Distribution (figs. 70, 73).—Western slope of the Andes of southern Peru in the departments of Arequipa, Moquegua and Tacna; altitudinal range from approximately 2300 to 4000 meters above sea level.

Characters.—Largest race of *Phyllotis darwini;* color intermediate between *rupestris* and *posticalis;* dorsal surface buffy or ochraceous finely pointed with black; head and shoulders sometimes contrastingly paler than back; underparts grayish, usually washed with buffy and with the plumbeous basal color of the hairs showing through; pectoral spot or streak present and well defined; tail bicolor, thinly to moderately haired and shorter to longer than head and body combined, average 103 per cent (80–119, 22 specimens). Auditory bullae moderately inflated, average anteroposterior length, less tubes, about 5.1 mm. (4.8–5.3, 18 specimens), and always less than alveolar length of molar row; mesopterygoid fossa comparatively broad with anterior border square or slightly rounded, rarely pointed as in *definitus*, posteromedian palatal spine hardly or not at all developed; posterolateral palatal pits anteriad to posterior border of palate; supraorbital region usually with a median sulcus, sometimes flattened, edges sharp or rounded, pinched upward or divergent and sometimes forming narrow ledges posteriorly; proximal ends of nasals pointed to truncate and terminating from slightly behind to slightly in front of fronto-premaxillary sutures; combined alveolar length of molars in adults, 6.1 mm. (5.7–6.8, 22 specimens) or 19 per cent (17–20) of greatest skull length.

Variation.—Topotypes and other specimens from localities near Arequipa (Yura; Tingo; Mt. Misti) are palest with pectoral streaks well defined. A series of three grayish brown individuals from Chihuata, 3125 meters altitude and about 3 kilometers east of Arequipa, is darkest, the pectoral streaks extremely weak, the tails more hirsute than in the preceding. Eleven specimens of *magister* taken near Tarata, Tacna, at altitudes ranging from 11,000 to 12,800 feet, are as pale as the Arequipa *magister* and slightly darker throughout than eleven specimens of *rupestris* variously collected between 11,500 feet and 13,500 feet in the same area. A distinct pectoral streak is present in all the *magister* but in only two *rupestris* from 13,200. Three *magister* and six *rupestris* from Río Torata, Moquegua, altitude 12,200 feet, are slightly paler than their respective relatives of the above-mentioned localities, the *rupestris* more markedly so than the *magister*. Palest individual of *magister* is an old male from Yura, near Arequipa, with grayish mottled head and shoulders. It is slightly darker than the average of a sympatric series of 29 *rupestris*. None of the Yura *rupestris* has a pectoral streak, tails of all are hairier, and one, with gray shoulders and head grayish as in the Yura *magister*, has completely white underparts.

P. d. magister averages slightly larger than *posticalis* but proportions of external cranial characters are approximately equal in both races. The largest *magister* at hand is slightly smaller than the largest *posticalis* but the smallest adult *magister* is appreciably larger than the smallest adult *posticalis* (cf. Tables 16, 19, pp. 286, 295).

Nasals are generally expanded anteriorly in *magister* but in three topotypes they are tapered as in most *rupestris;* supraorbital region pinched, or broad and flat, the edges sometimes slightly divergent and forming narrow ledges (cf. MVZ 115792, Río Torata; MVZ 115883, Tarata; compare with *caprinus* and *wolffsohni*); posterolateral palatal pits described as large by Pearson (1958, p. 429) appear to me to be as small as in comparable series of any taxon of the *Phyllotis darwini* group. In no specimen of *magister*, as here defined, are the pits as large as in any of the four known specimens of *Phyllotis darwini definitus*. Mesopterygoid fossa in one specimen of *magister* from Tarata, Tacna, is asymmetrically pointed in front; in the remaining skulls the anterior border of the fossa is square or rounded, the pterygoid processes parallel-sided or slightly divergent posteriorly; bullar tubes are relatively short with ventral surface generally convex.

Molars are actually (but not relatively) larger in *magister* than in other races; first primary fold of $m^{\underline{2}}$ usually persistent in moderately worn tooth, occasionally in moderately worn $m^{\underline{3}}$; second molar with a modified S- to 8-shaped pattern; $m^{\underline{3}}$ usually with *pf* 2 reduced to an enamel island. The mid-shaft area of all bacula examined is thickened (fig. 7). The same feature appears occasionally in other groups of the species.

Taxonomy.—There is no evidence of intergradation between *magister* and *rupestris* in two known areas of contact in southwestern Arequipa (Arequipa; Yura), one in western Moquegua (Torata) and one in eastern Tacna (Tarata, 3 sites at 11,500, 12,200, 12,800 feet, respectively). Each series of *magister* from each trap line is readily distinguished from its sympatriot (or perhaps compatriot) of presumably the same trap line, by overall larger size, darker color, well-defined pectoral streak and slightly less hairy tail (Table 17, p. 291). There are too few samples, however, to give assurance that complete reproductive isolation prevails at these critical points. All characters of *magister*, whether singly or in combinations, are of common occurrence throughout the range of *Phyllotis darwini*. Individuals practically indistinguishable from *magister* appear in Peru (*posticalis*), Bolivia (*wolffsohni*), northern Argentina (*caprinus*), southern Argentina (*xanthopygus*) and Chile (*darwini*). Most of these large, *magister*-like individuals or populations have no direct contact with the populations so named. Arequipa *magister*, however, does merge both morphologically and geographically with Ayacucho and Apurimac *posticalis*. It is also evident from material at hand

TABLE 17.—Comparisons of *Phyllotis darwini magister* (*m*) with sympatric *Phyllotis darwini rupestris* (*r*)

Locality	Head and body	Tail	Skull, greatest length	Alveolar length of molar row	Ratio molars: skull	Pectoral streak[10]	Pilosity of tail[11]	Body color[12]
Arequipa(*m*)	152[1]	158	36.8	6[2]	—	?	?	?
Arequipa(*m*)	118[3],118[4],138[5],124[6]	118,128,109,106	31.3,—,32.3,32.6	6.0,6.1,6.0,6.2	19,—,19,19	SS	HH	DD
Arequipa(*r*)	104[7],105[8]	124,—	28.6,—	5.0,5.3	17,—	ss	hh	dd
Yura(*m*)	144	138	32.0	6.3	20	S	H	D
Yura(*r*)	107(98–125)24	115(94–128)24	28.7(28.0–30.2)21	5.2(4.9–5.6)23	18.5(17–20)24	ss	hh	dd
Torata(*m*)	108,108,122	127,127,145	29.9,30.9,30.9	5.7,6.2,6.0	19,20,19	SS	HH	DD
Torata(*r*)	103(91–123)6	114(105–124)6	29.1(28.0–30.7)6	5.2(5.0–5.3)6	17(17–18)6	ss	hh	dd
Tarata 11,500(*m*)	133,131,127	130,134,143	31.6,32.1,32.8	6.0,5.9,6.8	19,18,20	SS	HH	DD
Tarata 11,500(*r*)	99,94,103	113,111,102	27.7,28.0,28.6	4.9,5.0,5.2	17,17,18	ss	hh	dd
Tarata 12,200(*m*)	131	143	32.9	5.7	17	S	H	D
Tarata 12,200(*r*)	101[9]	107	30.8	5.4	18	ss	hh	dd
Tarata 12,800(*m*)	110,142,144	131,154,156	30.1,33.2,34.5	5.9,5.9,6.4	20,18,19	SS	HH	DD
Tarata 12,800(*r*)	113,112,128,123	118,118,119,114	29.5,29.9,30.2,31.6	5.5,5.4,5.5,5.6	19,18,18,18	ss	hh	dd

[1] Type of *magister*, measurements from original description.

[2] Probably not a comparable measurement, and ratio to skull length, 16%, is omitted from the Table.

[3] Mt. Misti, collected 31 May, 1899, by P. O. Simons.

[4] Topotype, collected 28 May, 1899, by P. O. Simons.

[5] Collected 9 November, 1929, by Anthony and Ottley.

[6] Tingo, collected 11 June, 1926, by G. H. H. Tate.

[7] Collected 26 May, 1899, by P. O. Simons.

[8] Collected 30 May, 1899, by Perry O. Simons.

[9] Measurements of adult; characters of last three columns include those of a juvenal.

[10] SS = present in all.
ss = absent in all.

[11] HH = comparatively thinly haired in all.
hh = slightly longer or more thickly haired in all.

[12] DD = comparatively darker in all.
dd = more or less paler in all.

that *rupestris* in departing from the area of sympatry becomes larger and darker in northeastern Arequipa (*chilensis* of Pearson, cf. Cailloma series), and grades into the same peripheral populations of *posticalis* (fig. 73).

P. darwini limatus of the southwest coast of Peru is another annectant form. It more nearly resembles *magister* than *rupestris* of southern Peru by its larger size, tail proportionately longer, underparts darker, sometimes with a faint pectoral streak. *P. d. limatus* grades into *posticalis* but its precise geographic relationship with *magister* is unknown.

Intergradation between *magister* and *posticalis* is best illustrated with a series of three specimens collected by Pearson at Chihuata, about 14½ kilometers east of Arequipa. The specimens are in old pelage and sensibly darker, their pectoral streaks much weaker than in other examples of *magister* from the Arequipa region. These Chihuata *magister* are virtually indistinguishable from three specimens collected by Pearson in the vicinity of Puquio, Ayacucho, and identified by him as *Phyllotis darwini posticalis*. The only notable difference of "significance" between the two series is the absence of a pectoral streak in two of the Puquio specimens and its mere indication in the third (MVZ 116024) by a few pale buff hairs. Resemblance between the Chihuata *magister* and a series of five specimens from Puente Pajonal, Ayacucho, and another of the same number from Palmira, Apurimac, with pectoral streaks better developed, is complete enough to make distinctions between *magister* and southern populations of *posticalis* an arbitrary matter.

Phyllotis darwini posticalis, as now understood, is a composite of discrete *magister*-like and *rupestris*-like populations which interbreed at points of contact throughout most of the range. In southeastern Peru, where the *magister* and *rupestris* types diverge more from each other, interbreeding seemingly does not occur and the two forms behave and appear as distinct species at known points of contact. *Magister* represents the end of the speciation ring in *posticalis*. Farther south, in Chile and northern Argentina, fully interbreeding pockets of large and small populations reappear. Some have received distinctive names (*vaccarum*, *ricardulus*, etc.) but all are treated here as members of a single race, *rupestris*.

Phyllotis definitus Osgood was classified by Pearson as a subspecies of *Phyllotis magister* on the basis of large size and correspondingly large molars. The same characters, however, are shared with all other large members of the *darwini* group. The real differences between *magister* and *definitus* (cf. following section and p. 297) are accentuated by a geographic gap of 1100 kilometers which is largely occupied by *Phyllotis darwini posticalis.* Whatever the relationship between *magister* and *definitus* it can be derived only from their common relationship with *posticalis.* That *definitus* grades into *posticalis* is demonstrated elsewhere. It is shown now that *magister* also combines so intimately with populations of *posticalis* less than 300 kilometers away (Puquio; Yura and Chihuata) that no line of separation can be drawn between the two forms.

A parallel morphological and geographical relationship exists between *magister* and *wolffsohni* of the eastern Andes of Bolivia. Pearson (1958, p. 431) pointed to the situation but dismissed the possibility of subspecific relationship between the transandean forms. It is shown in the following section and in the account of *wolffsohni* that no real differences separate the two forms and that intergradation takes place through geographically intermediate *rupestris* and *caprinus* (fig. 77).

Remarks.—According to Thomas, the type of *magister* was "caught at the same place [i.e., Arequipa] as a number of examples representing the northern form of *Ph. darwini.*" Corroborating evidence of sympatry was gathered by Pearson (1958, p. 400). He observed that "*Phyllotis magister magister* is sympatric on the Pacific slope of southern Peru between 7,000 and 13,000 feet with *P. darwini rupestris*, one of the smallest of the subspecies of *darwini.* In the three areas where *P. magister magister* has been taken (Departments of Arequipa, Moquegua, and Tacna), *darwini* shares its habitat but unlike *magister* ranges besides into the more scantily vegetated desert at lower elevations and onto the altiplano at higher elevations. Actually, *darwini* tends to avoid the densest brush. I have taken *magister* only in the zone of maximum vegetation on the Pacific slopes of southern Peru, a zone where bushes and cacti form a relatively thick cover. In a collection made between January 23 and 27, 1952, at various elevations above Tarata, Department of Tacna, the two species were represented in the ratios shown in Table 2. If traps had been set at even lower altitudes, the catch of *magister* would presumably have decreased and that of *darwini* increased."

The cited Table 2 is reproduced in my Table 18. The interpolations in brackets are explained in the text.

I cannot understand the logic behind Pearson's conclusion that at levels lower than 11,000 feet "the catch of *magister* would presumably have decreased and that of *darwini* increased." Elsewhere

TABLE 18.—Altitudinal distribution of *Phyllotis darwini magister* Thomas and *P. darwini rupestris* Gervais captured above Tarata, Department of Tacna, Peru (Table 2, *ex* Pearson, 1958, p. 400).

Elevation (in feet)	Number of *magister*	Number of *darwini*
[15,200]	[0]	[1]
14,600	0 [0]	12 [5]
13,600–13,200	0 [0]	6 [3]
[13,000]	[0]	[2]
12,800	7 [3]	5 [5]
12,200	3 [1]	6 [2]
11,500	14 [3]	10 [4]
11,000	7 [4]	0 [0]
[Totals	31 (11)	39 (22)]

in the same region Pearson had taken *magister* together with *rupestris* at altitudes as low as 7000 feet. Furthermore, figures in Pearson's Table 2 (Table 18, above) showing the number of specimens taken at each station above Tarata may be questioned. The interpolated figures in brackets alongside those quoted represent the actual number of specimens listed by Pearson (1958, pp. 417, 418, 431) as "Specimens examined" from the altitudinal stations shown. The total of *magister* and *darwini* in Table 2 (Table 18) is 31 and 39, respectively. In his "Specimens examined" section, Pearson lists only 11 and 22 specimens, respectively, from the same stations. The last pair of figures agrees with the number of specimens made available to me for study by the Museum of Vertebrate Zoology. The Tarata material was collected from 23–28 January, 1952. The field numbers for the Tarata series of *magister* and *darwini* combined run from a low of 738 to a high of 755 (A. K. Pearson) and a low of 3546 to a high of 3566 (O. P. Pearson). If all numbers in the two series were of specimens of *magister* and *darwini*, assuming no other kinds of animals were taken, the totals would be 39 or still 31 less than the totals in Pearson's Table 2. Unless the figures of his Table 2 include specimens first identified in the field and then discarded, no credence can be placed in them.

The statistical analysis of the measurements of *magister* compared with sympatric populations of *darwini* given by Pearson in his figure 9 (p. 430) also raises questions. In his "Specimens examined," Pearson lists a total of 8 *magister* and 11 *darwini* (i.e., *rupestris*) from Arequipa proper. Presumably all are of the original Simons 1899 collection. The measurements given in Pearson's figure 2, how-

TABLE 19.—Measurements of *Phyllotis darwini magister* Thomas

Locality	Head and body	Tail	Hind foot	Ear
Arequipa[1]	152	158	32	29
Arequipa	118,138	128,109	28,28	27,—
Mt. Misti	118	118	27	26
Chihuata	135,134,143	129,134,122	27,28,29	27,27,25
Tingo	124	106	27	—
Yura	144	138	28	27
Río Torata	108,108,122	127,127,145	27,28,29	24,26,25
Tarata, 1 km. N	118,121,133,135	124,125,131,129	27,28,28,29	26,25,26,24
Tarata, 2 km. N	133,131,127	130,134,143	28,28,29	25,25,25
Tarata, 3 km. N	131	143	30	25
Tarata, 4 km. N	110,142,144	131,154,156	29,28,32	24,26,29

Locality	Weight	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
Arequipa[1]		36.8	18.5	6.0
Arequipa	—	—,32.3	—,16.0	6.1,6.0
Mt. Misti	—	31.3	15.7	6.0
Chihuata	67,66,88	32.6,33.3,34.2	16.5,17.0,16.7	6.0,6.1,6.0
Tingo	—	32.6	15.5	6.2
Yura	—	32.0	16.8	6.3
Río Torata	—	29.9,30.9,30.9	15.7,15.8,15.9	5.7,6.2,6.0
Tarata, 1 km. N	58,55,93,71	31.3,31.8,33.4,34.5	16.2,16.4,17.4,17.9	6.1,6.1,6.3,5.9
Tarata, 2 km. N	70,58,75	31.6,32.1,32.8	16.6,16.2,17.1	6.0,5.9,6.8
Tarata, 3 km. N	72	32.9	16.7	5.7
Tarata, 4 km. N	44,65,89	30.1,33.2,34.5	16.2,17.1,17.0	5.9,5.9,6.4

[1] Type of *magister*; measurements from original description.

ever, are for 15 *magister* and 37 *darwini*. Obviously, Pearson included other "Arequipa region" specimens which may or may not be sympatric and synchronic. Similarly, 13 Tacna and Moquegua *magister* are collectively compared with 9 *darwini* from the same Departments.

Measurements.—See Table 19 (p. 295).

Specimens examined.—22. PERU—*Arequipa:* Chihuata, 2 miles east, 3 (MVZ); Arequipa, 2 (AMNH; CNHM); Mt. Misti, 1 (CNHM); Tingo, 1 (AMNH); Yura, 1 (CNHM). *Moquegua:* Río Torata, 15 km. NE of Torata, 3 (MVZ). *Tacna:* Tarata, 11 (MVZ).

Phyllotis darwini definitus Osgood

Phyllotis definitus Osgood, 1915, Field Mus. Nat. Hist., Zool. Ser., **10**: 189.

Phyllotis magister definitus, Pearson, 1958, Univ. Cal. Publ. Zool., **56**: 431—*Ancash* (Macate); taxonomy.

Type.—Adult male, skin and skull, Chicago Natural History Museum no. 21125; collected 14 February, 1914, by M. P. Anderson.

Type locality.—Macate, north-central Ancash, Peru; altitude, approximately 2800 meters.

Distribution (figs. 70, 73).—Known from type locality only.

Characters.—More brown than *posticalis* or *rupestris*, molars larger; dorsal surface warm brown, the anterior half slightly grizzled; underparts washed with ochraceous and not sharply defined from sides; a well-defined pectoral patch present; bicolor tail subequal to or shorter than combined head and body length; auditory bullae moderately inflated, antero-posterior length, less tubes, about 5.0 mm. (4.7–5.1, 4 specimens) and less than alveolar length of molar row; bullar tubes short and with a pronounced keel on ventral surface; anterior border of mesopterygoid fossa pointed; posterior median border of palate without spinous process; posterolateral palatal pits large and on a line with or anteriad to anterior border of mesopterygoid fossa; supraorbital edges rounded, the ridges hardly raised; proximal ends of nasals truncate and terminating on a line with or slightly behind premaxillary sutures; molars large, combined alveolar length, 6.0–6.2 mm. (4 specimens) or 19–20 per cent of greatest skull length.

Variation.—Most of the slight amount of individual variation noted is detailed in the characterization of the subspecies. It must be emphasized that *definitus* is based on four specimens representing a single age group of a single crop.

TABLE 20.—Measurements of *Phyllotis darwini definitus* Osgood

Macate	Head and body	Tail	Hind foot	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
C 21125 ♂[1]	131	132	28	31.8	16.8	6.3
C 21126 ♀	124	120	27	30.2	16.2	6.1
C 21127 ♀	135	124	28	32.2	16.2	6.2
C 21128 ♀	121	111	29	30.7	16.1	6.0

C=Specimens in Chicago Natural History Museum.

[1] Type.

Taxonomy.—Present classification of *Phyllotis definitus* as a subspecies of *P. darwini* nearest related to *posticalis* depends partly on negative evidence. Morphological intergradation between *definitus* and *posticalis* can be demonstrated. There is no reason to believe that geographical intergradation does not occur also. Pearson (1958, p. 414) postulated that "collecting in north-central Peru will probably reveal *posticalis* or some other race of *darwini* in the high mountains of Ancash." This "other race of *darwini*" can be no other than *definitus*. Pearson, however, treated *Phyllotis definitus* together with *Phyllotis magister* as a species distinct from *darwini*. Except for parallel development in size, there is nothing to support this thesis. *Definitus* and *magister* are separated by a geographical gap of 1100 kilometers and intergradation between the two can be effected only through the geographically and morphologically intermediate *Phyllotis darwini posticalis*.

Phyllotis darwini definitus is much larger and heavier than sympatric *Phyllotis andium*, more richly colored brown, underparts more ochraceous with a well-defined pectoral patch always present, tail bicolor to tip; anterior border of mesopterygoid fossa not rounded or square, the palate relatively narrower with well-marked longitudinal ridges. Allopatric individuals of *andium* of equal body size are more lightly built with smaller crania and molars. Specimens of *P. darwini posticalis*, on the other hand, commonly equal and even exceed the size and bulk of *definitus* and in many the molars are as large. However, the short, thick rostrum and pointed anterior border of the mesopterygoid fossa characteristic of *definitus* are uncommon in *posticalis*. Huancavelica representatives of *posticalis*, notably a series of four specimens from Lircay, most nearly resemble the four known specimens of *definitus*.

Measurements.—See Table 20.

Specimens examined.—4 including the type, all from Macate, Ancash, Peru (CNHM).

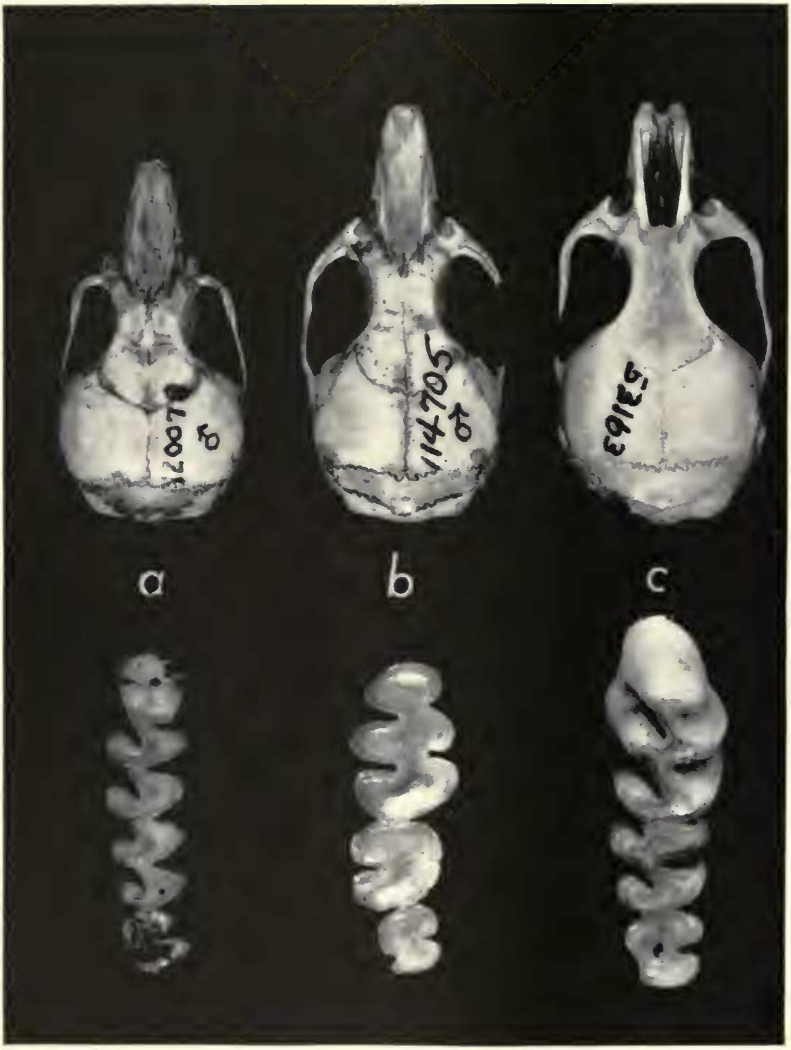

FIG. 82.—Age-size variation in *Phyllotis darwini limatus:* *a*, skull and molars of a juvenal from 4 miles east of Santa Eulalia, Lima, Peru; *b*, extremely old individual from 3 miles west of Atico, Arequipa; *c*, juvenal from Hacienda San Jacinto, Ica, Ica. (Skulls about × 2; molars about × 10.)

Phyllotis darwini limatus Thomas

H[esperomys] Darwinii, Tschudi, 1844, Fauna Peruana, 1: 16, 181, 184—PERU: *Lima* (Huacho).

Phyllotis darwini limatus Thomas, 1912, Ann. Mag. Nat. Hist., (8), **10**: 407—part, type only. Pearson, 1958, Univ. California Publ. Zool., **56**: 413—PERU: *Arequipa* (Atico; Chucarapí; Tambo); *Ica* (Ica); *Lima* (Chosica; Huinco; La Palma; Naña; Oscolla; Rimac Valley; San Bartolomé Station; Santa Eulalia; Surco; Verruga Canyon; Yaca).

Type.—Male, skin and skull, British Museum (Natural History) no. 0.5.7.43; collected 29 January, 1900, by Perry O. Simons.

Type locality.—Chosica, near Lima, Peru; altitude, 850 meters.

Distribution (figs. 70, 72, 73).—Coast and foothills of the western slope of the Andes of Peru in the departments of Lima, Ica and Arequipa. The range may continue along the coast into northern Chile where intergradation with *P. d. darwini* may occur (cf. Pearson, 1958, p. 421).

Characters.—General color and body size as in *rupestris*, tail proportionately longer; head grayer than trunk; lateral line not always well defined and rarely continuing around base of rump; underparts sharply defined whitish to dirty gray lightly washed with buff; a weakly marked pectoral streak sometimes present; tail bicolor, well-haired with well-developed pencil and nearly always longer than head and body combined (tail: head and body=118 [98–126]: 100, 25 specimens); auditory bullae well inflated, antero-posterior length, less tubes, subequal to or, usually, longer than alveolar length of molar row; other cranial characters as in *rupestris;* enamel pattern of $m^{\underline{2}}$ usually more S- than 8-shaped (fig. 82); first primary fold of moderately worn $m^{\underline{2}}$ well defined and, usually, at least indicated in moderately worn $m^{\underline{3}}$; second primary fold of m^{3} much more frequently open to the margin than forming an enamel island; alveolar length of molar row 4.6–5.2 or 17–18 per cent of greatest skull length.

Variation.—The palest samples are from Ica and western Arequipa (Chucarapí; Atico), the darkest are seven specimens from Chosica collected in August, 1955, by O. P. Pearson. In contrast, a series of three specimens from the same general locality taken in January 1942, by C. C. Sanborn, are more buff, less gray on upper parts and distinctly less gray on underparts. In all, they resemble more nearly the palest representatives of the race from Ica and Arequipa than they do their topotypes. Pearson alludes to the difference in color by remarking that his "specimens captured in 1955 in relatively wild parts of the Rimac Valley [Chosica; San Bartolomé; Rimac Valley; Surco; Naña; Santa Eulalia] have grayish bellies reminiscent of those mice living in houses. This discoloration may be due to smoke from the railroad and from the annual burning of cotton plants in the valley." Whatever the cause, a test with detergents proves that even with grime removed the darker color of the underparts persists as a character of Pearson's specimens from Chosica, "Rimac Valley," San Bartolomé and Surco. Underparts of the three specimens from Naña in the Rimac Valley are whitish and those of the five specimens from Santa Eulalia are intermediate. All series in question with underparts washed or unwashed can be precisely matched in color with series from temperate zone localities in various parts of Peru and northern Chile where neither railroads nor cotton plant burning occurs. It is interesting to compare Pearson's explanation for the difference in color between the allochronic Chosica series and the somewhat analogous Salinas series of *rupestris* (cf. p. 308).

Two specimens collected 19 March, 1951, in Atico, Arequipa, by O. P. Pearson are in new buffy pelage while two specimens taken 20 May, 1952, are in old worn and distinctly redder pelage.

The terminal portion of the tail is marked by a white band in the type of *limatus* (Chosica, Lima, Peru) and two of ten topotypes examined. It also occurs in one of five specimens from "Rimac Valley," in one of two specimens collected at Naña, one in Surco and in the single specimen from Oscolla, all localities in the Rimac Valley above Lima. The latter (CNHM no. 53056) was captured alive 28 December, 1941, and kept in a laboratory in Lima until its death, 10 February, 1942. It is remarkable for white patches on the upper surface of the distal fifth of its tail, and the unusual color of its body. The anterior half of the upper parts is pale as in average Arequipa *rupestris* or *limatus*, the posterior half more warmly colored than in any *rupestris* or *limatus*. The general coloration may represent that of the wild Oscolla population but this is unlikely. No specimen from other localities in the same general region resembles it. Possibly the color pattern was evoked by the unnatural laboratory environment. The Surco individual (MVZ 120033) with braincase monstrously enlarged by hydrocephaly has already been noted by Pearson (loc. cit.) and is figured here (fig. 80, *a*).

The well-defined first and second primary folds in the molars of *P. darwini limatus* is a character common to most representatives of *P. darwini* of western Peru and northern Chile.

Table 21.—Measurements of *Phyllotis darwini limatus* Thomas

Locality	Head and body	Tail	Hind foot	Weight	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
PERU								
Lima								
Chosica[1]	115	150	25		28	31.4	16	4.8
Chosica[2]	113,114	135,140	27,27		—,27	29.4,29.6	15.3,15.3	5.4,5.2
Chosica	115(107–122)5	135(126–148)4	26(25–26)5		26(25–27)4	30(29.6–30.4)4	15.2(15.0–15.5)5	5.3(5.2–5.5)5
San Bartolomé	110,118	131,128	27,27		27,26	29.9,30.1	14.8,15.3	5.0,5.2
Naña	114,116	144,139	26,27		27,27	—,29.5	15.0,14.7	5.0,5.2
Rimac	110(103–120)40	131(124–146)4	26(25–27)4		26(25–27)4	29.5(28.5–30.6)4	14.8(14.3–15.2)4	5.1(5.0–5.2)4
Santa Eulalia	110,111,110	124,132,134	26,26,26		27,27,27	29.7,29.8,29.9	14.5,15.0,15.1	5.2,5.3,5.2
Surco	96	110	25		24	27.5	15.2	5.0
Ica								
San Jacinto[2]	116	136	28		27	29.6	15.1	5.5
Arequipa								
Atico	112(102–121)4	125(115–138)4	25(24–27)4	41(30–49)4	27(25–28)4	29.7(28.3–31.7)4	14.9(14.4–15.4)4	5.2(5.0–5.5)4
Chucarapí	97,	115,—	23,23	27,26	26,27	27.1,29.0	13.9,14.4	4.8,5.2

[1] Type of *limatus* Thomas; measurements from original description.

[2] Subadult.

There is no consistent correlation between skull size and molar wear in individuals of different series. A juvenal from Santa Eulalia, Lima, with greatest skull length of 25.4 and alveolar length of molar row 4.9, has slightly more worn first and second molars than another juvenal from Ica with skull 30.5 and alveolar length 5.4. This last, in turn, is appreciably larger than an apparently old and fully grown individual from Chucarapí, Arequipa, with skull 29.5, molar row 4.9 and crowns more worn than those of all but one of the 36 specimens of *limatus* at hand (fig. 82).

The difference in size and tooth wear between examples cited above is ostensibly related to the quantity, quality and availability of nourishment in the habitat of each.

Taxonomy.—Phyllotis darwini limatus Thomas was originally described as the "northern representative of *Ph. darwini* [but] paler and [with] longer tail than the typical Chilean form. Specimens referable to it are in the [British] Museum from various parts of the highlands of Peru and Bolivia, including Caylloma, Arequipa, La Paz, etc." In effect, *limatus* of Thomas, as originally conceived, is equivalent to *rupestris* Gervais, a name which, at the time, was linked with the genus *Akodon* and therefore not taken into account. Pearson (1958, p. 413) redefined *limatus* and restricted it to its present range along the coast and Andean foothills of Peru. He suggests that *limatus* "may intergrade with *P. d. posticalis* on the west slope of the Andes somewhere south of the Rimac Valley (central Lima) . . . but in the valley it is separated from *posticalis* by a zone of brush occupied by *Phyllotis andium*." He also believes that *limatus* "probably intergrades with the more inland *P. d. rupestris* in some valleys in the department of Arequipa and possibly in northern Chile."

Measurements.—See Table 21.

Specimens examined.—37. PERU: *Arequipa:* Atico, 3 miles west, 4 (MVZ); Chucarapí, Tambo Valley, 2 (MVZ). *Ica:* Hacienda San Jacinto, 2 (CNHM). *Lima:* Chosica, 10 (CNHM, 3; MVZ, 7); Naña, 2 (MVZ); Oscolla, 1 (CNHM); Rimac Valley, 5 (MVZ); San Bartolomé Station, 4 (MVZ); Santa Eulalia, 5 (MVZ); Surco, 1 (MVZ); Veruga Canyon, 1 (MCZ).

Phyllotis darwini rupestris Gervais

Mus rupestris Gervais, 1841, Voy. "Bonite," Zool., **1**: 51. Gervais, 1841, Bull. Soc. Philom., Paris, p. 115—"BOLIVIA" [=Chile]: *Antofagasta* (Cobija, skeleton only). Gay, 1847, Hist. Chile, Zool., **1**: 115, atlas, pl. 6, fig. 1 (skull and dentition), pl. 7 (animal figured not the type, may be *Phyllotis darwini darwini*).

M[us (Abrothrix)] rupestris, Gervais, 1849, Dict. Univ. Hist. Nat., **10**: 731—characters; classification.

Abrothrix rupestris, Lesson, 1842, Nouv. Tabl. Reg. Anim., p. 136—classification.

Phyllotis darwini rupestris, Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 205-6—taxonomy; CHILE: *Antofagasta* (San Pedro de Atacama; 20 miles east of San Pedro, Río San Pedro); BOLIVIA: *Potosí* (Lipez); ARGENTINA: *Jujuy* (Casabindo). Mann, 1945, Biológica, Trab. Inst. Biol. Univ. Chile, fasc. **2**, p. 39—CHILE: *Tarapacá* (Valley of Oases; Pampa of Tamarugal). Mann, 1950, Investigaciones Zool. Chilenas, fasc. **2**: 5—CHILE: *Tarapacá*. Pearson, 1958, Univ. California Publ. Zool., **56**: 417—revision; distribution [for locality records see p. 244].

Mus capito Philippi, 1860, Reise durch die Wüste Atacama, p. 159, Zool., pl. 2, fig. 2 (animal), pl. 5, fig. *c* (skull)—CHILE: *Antofagasta* (type locality, Hueso Parado, near Taltal); name preoccupied by *Mus capito* Olfers, 1818, an *Oryzomys*. Philippi, 1900, Anal. Mus. Nac. Chile, Zool., Ent., **14a**: 10, pl. 1, fig. 2 (animal)—characters.

Hesperomys glirinus Philippi, 1896, Anal. Mus. Nac. Chile, Zool., Ent., **13a**: 19, pl. 7, fig. 3 (animal, feet, molars)—CHILE: *Antofagasta* (type locality, San Pedro de Atacama).

Mus glirinus, Philippi, 1900, Anal. Mus. Nac. Chile, Zool., Ent., **14a**: 59—characters.

Hesperomys lanatus Philippi, 1896, Anal. Mus. Nac. Chile, Zool., Ent., **13a**: 19, pl. 7, fig. 2 (animal, skull, molars)—CHILE: *Antofagasta* (type locality, San Pedro de Atacama).

Mus lanatus, Philippi, 1900, Anal. Mus. Nac. Chile, Zool., Ent., **14a**: 59—characters.

Phyllotis arenarius Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9**: 224—BOLIVIA: type locality, Uyuni, Potosí, altitude, 3670 meters; *Oruro; Sucre; Potosí;* PERU: *Arequipa*. Thomas, 1913, op. cit., (8), **11**: 139—ARGENTINA: *Jujuy* (Cerro de Lagunita, 4500 meters). Yepes, 1933, Rev. Chilena Hist. Nat., **37**: 47—ARGENTINA: *Catamarca* (Laguna Blanca); *Los Andes* (San Antonio); *Jujuy* (Sierra de Zenta).

Ph[yllotis] arenarius, Yepes, 1935, Rev. Inst. Bacteriol., **7**: 223—characters; distribution.

[*Phyllotis lutescens*] *arenarius*, Osgood, 1944, Field Mus. Nat. Hist., Zool. Ser., **29**: 194—classification.

Phyllotis darwini vaccarum Thomas, 1912, Ann. Mag. Nat. Hist., (8), **10**: 408—ARGENTINA: type locality, Las Vacas, Mendoza, 2500 meters; *Mendoza* (Puente del Inca).

Phyllotis darwini vaccarum, Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 205—characters; distribution; CHILE: *Coquimbo* (Baños del Toro: Paiguano); *Atacama* (Domeyko); ARGENTINA: *Neuquén* (Chos Malal); *Mendoza* (Punta Vaca). Yepes, 1935, Rev. Inst. Bacteriol., **7**: 223, pl. 4, fig. 2 (animal)—characters. Yepes, 1936, Nov. Reunion Soc. Argentina Patol. Reg. en Mendoza, Publ. **31**: 710—ARGENTINA: *Mendoza* (Malargüe [Cañada Colorada]). Pearson, 1958, Univ. California Publ. Zool.,

56: 419—revision; synonyms, *oreigenus* Cabrera, *wolffhuegeli* Mann; distribution [for locality records see p. 244].

Phyllotis ricardulus Thomas, 1919, Ann. Mag. Nat. Hist., (9), **3:** 493—ARGENTINA: type locality, Otro Cerro, 45 km. west of Chumbicha, "Rioja" (=Catamarca), 3000 meters. Thomas, 1919, op. cit., (9), **4:** 130—part; ARGENTINA: *Jujuy* (Abrapampa; Casabindo). Thomas, 1920, op. cit., (9), **6:** 417—ARGENTINA: *La Rioja* (La Invernada; Potrerillos). Thomas, 1921, op. cit., (9), **8:** 611—ARGENTINA: *Jujuy* (Sierra de Zenta). Thomas, 1926, op. cit., (9), **18:** 194—part; BOLIVIA: *Potosí* (Lipez). Yepes, 1935, An. Mus. argentino Cienc. Nat., **38:** 335—ARGENTINA: *Jujuy* (La Laguna). Yepes, 1936, Physis, **12:** 37—ARGENTINA: *La Rioja* (San Antonio; Puesto Viejo; Chilicito; Las Piriquitas).

[*Phyllotis darwinii*] *ricardulus*, Osgood, 1944, Field Mus. Nat. Hist., Zool. Ser., **29:** 194—"most of the specimens referred by Thomas to his *ricardulus* probably should be called *rupestris*."

Phyllotis darwini ricardulus, Pearson, 1958, Univ. California Publ. Zool., **56:** 418—revision; ARGENTINA: *Catamarca* (Chumbicha; Otro Cerro); *Los Andes* (San Antonio de los Cobres); *Salta* (G. M. Sola; Incamayo).

Phyllotis oreigenus Cabrera, 1926, Rev. Chilena Hist. Nat., **30:** 319, fig. 42 (molars)—ARGENTINA: type locality, Laguna Blanca, Catamarca, 3100 meters; *Los Andes* (Salar de Antafalla). Yepes, 1935, An. Mus. argentino Cienc. Nat., **38:** 335—listed.

Phyllotis wolffhuegeli Mann, 1944, Biológica, Trab. Inst. Biol. Univ. Chile, fasc. **1:** 102 (name), p. 108 (description), fig. 7 (alimentary canal), pl. 8 (alimentary canal), pl. 9 (skin), pls. 10, 11 (skull)—CHILE: type locality, Bocatoma, Lo Valdés, Cajón del Río Volcán, Santiago, 1800 meters.

Phyllotis osgoodi Mann, 1945, Biológica, Trab. Inst. Biol. Univ. Chile, fasc. **2:** 81, figs. 32–36 (anat.), pl. 30 (skin), pl. 31 (skull)—CHILE: type locality, Parinacota, puna of Tarapacá. Mann, 1950, Investigaciones Zool. Chilenas, fasc. **2:** 5—CHILE: *Tarapacá.*

Phyllotis arenarius chilensis Mann, 1945, Biológica, Trab. Inst. Biol. Univ. Chile, fasc. **2:** 84, figs. 37, 38 (alimentary tract), pl. 32 (skull), pl. 33 (skin)—CHILE: type locality, Parinacota, puna of Tarapacá. Mann, 1950, Investigaciones Zool. Chilenas, fasc. **2:** 5—CHILE: *Tarapacá.*

Phyllotis darwini chilensis, Pearson, 1958, Univ. California Publ. Zool., **56:** 415—revision; *osgoodi* Mann a synonym; distribution [see p. 244 for locality records].

Phyllotis Darwini, Cabrera, 1905, Rev. Chilena Hist. Nat., **9:** 16—part, *lanatus* Philippi and *glirinus* Philippi in synonymy.

Ph[*yllotis*] *darwini*, Thomas, 1912, Ann. Mag. Nat. Hist., (8), **10:** 406—PERU: *Arequipa.*

Phyllotis (*Phyllotis*) *darwinii* subsp., Pearson, 1951, Bull. Mus. Comp. Zool., **106:** 142—PERU: *Puno* (Santa Rosa; Caccachara; Juli; Pairumani).

Phyllotis darwini subsp., Thomas, 1921, Ann. Mag. Nat. Hist., (9), **8:** 216—ARGENTINA: *San Juan* (Tontal).

Phyllotis sp., Zuñiga, 1942, Bol. Mus. Hist. Nat. "Javier Prado," Año 6, no. 20: 393–396—PERU: *Lima* (Lomas near Lima).

Phyllotis Wolffsohni, Thomas (not Thomas, 1902), 1926, Ann. Mag. Nat. Hist., (9), **17**: 321—BOLIVIA: *Tarija* (Sama).

Phyllotis darwinii limatus, Thomas (part, not Thomas), 1912, Ann. Mag. Nat. Hist., (8), **10**: 407—PERU.

Phyllotis xanthopygus, Thomas and St. Leger (not Waterhouse) 1926, Ann. Mag. Nat. Hist., (9), **18**: 635—"*xanthopygus* . . . [may] grade into the original *Ph. darwini;* ARGENTINA: *Neuquén* (Chos Malal; Las Lajas). Thomas, 1927, op. cit., (9), **20**: 200—ARGENTINA: *Neuquén* (Collon Cura; Quilquihue).

Phyllotis darwini xanthopygus, Osgood (part, not Waterhouse), 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 208—ARGENTINA: specimen from Collon Cura, Neuquén, only. Pearson, 1958, Univ. California Publ. Zool., **56**: 420—part, ARGENTINA: *Neuquén* (Collon Cura; Las Lajas; Quilquihue).

Phyllotis nogalaris, Mann (not Thomas), 1950, Investigaciones Zool. Chilenas, fasc. **2**: 5—CHILE: *Tarapacá* (Esquina; Putre).

[*Phyllotis darwini*] *osilae*, Osgood (not J. A. Allen), 1944, Field Mus. Nat. Hist., Zool. Ser., **29**: 194—classification.

P[*hyllotis*] *darwini darwini*, Pearson (part, not Waterhouse), 1958, Univ. California Publ. Zool., **56**: 421 (in text), Appendix 1 (measurements)—*Antofagasta* (Paposa); *Atacama* (Vallenar); *Santiago* (Río Blanco).

Type.—Skeleton only, presumably in Muséum National d'Histoire Naturelle, Paris; collected 27 July, 1836, by M. Gaudichaud, during the "Voyage autour du Monde sur la Corvette 'La Bonite.' "

Type locality.—High mountains of Cobija, Antofagasta, northern Chile; specimens collected by Sanborn on the Río San Pedro, a tributary of the Loa, are regarded as typical by Osgood (1943, p. 207) and Pearson (1958, p. 417) and the type locality is here restricted accordingly.

Distribution (figs. 70, 73–75).—Southern Peru, southwestern Bolivia, northern Chile and northwestern Argentina, as follows: from the departments of Arequipa, Puno, Moquegua and Tacna in Peru, eastward into western Bolivia in the departments of La Paz, Oruro, Potosí and adjacent parts of Cochabamba, Chuquisaca and Tarija, thence southward into northern Argentina in the departments of Jujuy and western portions of Salta, Catamarca, La Rioja, San Juán, Mendoza and Neuquén; in Chile from Tarapacá to northern Coquimbo thence southward through the Andes into Santiago. The range includes desert, xerophytic scrub country and grassland or puna; altitudinal range from approximately 500 to 5000 meters above sea level or to the upper limits of plant growth.

Characters.—Palest and smallest race of *P. darwini;* dorsal surface buffy, finely ticked to heavily lined with the dark brown guard hairs; head and shoulders usually paler than dorsum; bright ochraceous lateral line generally present and often continuing around base of rump; underparts sharply to moderately well defined whitish or pale gray with slaty basal portions of hairs showing through, a buffy wash often present; pectoral streak usually absent (present and well defined in less than 10 per cent of specimens examined); tail averaging longer than combined head and body length (tail: head and body =81–132: 100), bicolor, well haired to nearly bushy, pencil well defined; auditory bullae moderately inflated, average antero-posterior length, less tubes, about 5.1 mm. (4.3–5.9, 345 specimens) and usually less than alveolar length of molar row; bullar tubes rarely elongate; mesopterygoid fossa measured at base of hamular processes usually narrow but sometimes (particularly in Bolivia and Chile) as wide as parapterygoid fossa measured at same plane; posterior border of palate rounded, notched or with a pair of processes which sometimes fuse into a single median spine; postero-lateral palatal pits usually situated anteriad to posterior border of palate, infrequently posteriad (Chile, Bolivia, Puna, Peru); supraorbital edge sharp or rounded, pinched anteriorly, rarely extended posteriorly as narrow shelves or ledges; fronto-parietal suture narrowly V-shaped to broadly arced, proximal ends of nasals pointed to truncate and terminating on a line with, often behind, rarely in front of, fronto-maxillary suture; alveolar length of molar row, in adults, 4.6–6.7 or 15–20 per cent of greatest skull length.

Variation.—A number of individual, local and specific variables in *rupestris* are discussed in the descriptions of neighboring races and, particularly, the sympatric forms of the sibling species *Phyllotis osilae* (*q.v.*).

Color phases in *rupestris* are more apparent than real. Whether pale gray, dark gray, buff, ochraceous or cinnamon all individuals in any large series are fully intergrading. Samples in different stages of molt usually differ markedly in color from each other, the older pelage being either redder, i.e., more ochraceous, or darker, more gray.

Palest populations occur in southwestern Arequipa. Slightly darker populations with more gray or ochraceous inhabit northern Chile, western Bolivia and northern Argentina. Darkest representatives of the race are from the upper altitudinal limits of the range in the Peruvian departments of Moquegua, Tacna and Puno. Humidity rather than altitude appears to be the controlling factor in color, the paler series having been taken either during dry season or in year round arid localities.

A direct correlation between altitude, i.e., temperature, and degree of intensity of pigmentation is not evident. An increase in the thickness and length of guard hairs at high altitude, however, does result in a darker-appearing coat. This can be illustrated with the series collected by Pearson on a mountain slope north of Tarata, Tacna, and listed in the following table.

TABLE 22.[1]—*P. d. rupestris* from successively higher altitudes north of Tarata, Tacna

Locality	Altitude in meters	Date collected	Total specimens	Classification ex Pearson (1958)
2 km. north	3600	23–25 Jan., 1952	4	*P. d. rupestris*
3 km. north	3812	25 Jan., 1952	2	*P. d. rupestris*
4 km. north	4000	26–27 Jan., 1952	5	*P. d. chilensis*
4.5 km. north	4125	26 Jan., 1952	1	*P. d. chilensis*
5 km. north	4220	26 Jan., 1952	2	*P. d. chilensis*
20 km. north	4562	28 Jan., 1952	5	*P. d. chilensis*
25 km. north	4750	29 Jan., 1952	1	*P. d. chilensis*

[1] Compare with Table 18.

In the Tarata series the density of the guard hairs becomes greater with increasing altitude although the difference between series of successive stations is slight. The cumulative effect, however, is that the six specimens from the two highest stations appear to be notably darker than the six from the two lowest. Real differences in color, however, are practically nil. The tone of the guard hairs, the buffy bands of the cover hairs and the lateral line are virtually the same at all stations. A heavier coat at higher, colder localities, is also noted in mice of other areas including Río Torata (not Tarata), Moquegua. Here specimens taken at 2940 and 3500 meters were classified by Pearson as *rupestris* while those with the more prominent dark guard hairs taken three miles away at 4280 meters were determined as *chilensis*. Color difference between these is no more real than in the Tacna series. Tacna mice referred to *rupestris* by Pearson are smaller but also appear to be younger than his Tacna *chilensis*. The material from Moquegua is wholly inadequate for an accurate appreciation of size differences, if any. A remarkable feature of Pearson's Tacna and Moquegua *rupestris* as compared with his *chilensis* of the same mountain sides, is the higher incidence of persistence in the former of a well-defined first primary fold in m^2 and, to a lesser degree, in m^3, in even well-worn teeth. This character, however, is highly variable and certainly related to fodder differences at different stations.

A well-defined pectoral streak is present in less than 10 per cent of all specimens examined. The character appears most frequently among specimens from the Department of Puno, with the greatest number (about 15 per cent of the total) from the area of sympatry with the sibling species *Phyllotis osilae* in which a pectoral streak is generally present.

Four specimens, including one juvenal, from the upper Río Maule, Talca, are exceptionally large and more nearly resemble some of the darker Peruvian *rupestris* (cf. Asilla, Puno) than the generally pale Argentine or Chilean members of the race. The series was collected by Colin C. Sanborn in a mining camp 14 kilometers above Curillinque. The oldest individual, a male, is larger than any other *P. darwini* examined by me. Its fractured skull (CNHM 50545), represented by anterior half and fragments of posterior portions, could have exceeded 36 mm. in greatest length. Its molar row of 6.7 mm. is exceeded only by that of a specimen of *P. darwini magister* with an alveolar length of 6.8 mm. Evidently living conditions for *Phyllotis* in the mining camp were extremely favorable. The discordant characters of the Río Maule series are, possibly, manifestations of niche variation.

Coats of a series of 11 specimens from Salinas, Arequipa, Peru, collected by Colin C. Sanborn and associates, vary strikingly from new and bright in color to old and somber. The darkest (CNHM 49487) collected 3 October, 1939, is not quite as heavily lined with black as the paler of two specimens in prime pelage collected by O. P. Pearson in the same locality at nearly the same altitude but on December 17 and 18, 1951. The difference in color led Pearson to suggest that Sanborn's series was "probably altered by treatment with borax or alum." This condemnation is unwarranted. The two Salinas series vary in the same way as, for example, the allochronic series of *P. darwini limatus* collected in Chosica, Lima, and Atico, Arequipa (cf. p. 300). Sanborn's series is no more or less discolored than his other material which includes the bulk of our southern Peruvian *Phyllotis*. All were prepared in a uniform manner with borax used as preservative and all, except the Salinas specimens, served without qualifications as bases for Pearson's fine discriminations between species and subspecies. That Sanborn's Salinas series averages *rupestris*-like in color rather than "*chilensis*"-like, as Pearson would desire, cannot be dismissed as an artefact. The 11 specimens were taken in a different year and season at a different locale and a different elevation from the two specimens collected by Pearson. Sanborn's series is paler because of a paucity of blackish guardhairs. It is also appreciably smaller in body size, a character which cannot be dismissed as extraneous. The differences between the

Sanborn and Pearson series may be examples of crop variation or may point to different genotypes. The Salinas population sampled by Pearson is certainly not the same and need not be a direct descendant of, the Salinas population sampled by Sanborn 12 years earlier. Another consideration is that if Pearson had collected more specimens, complete intergradation between the two allochronic series might be demonstrated. Indeed, a series of 24 specimens from Cailloma, Arequipa (4330 meters), shows an even greater range of variation in color. The palest is as pale as any of the Sanborn Salinas series and the darkest (CNHM 49510, 49519) are more heavily lined with black and more warmly colored ochraceous than Pearson's Salinas specimens.

A short but well-defined first primary fold is normally present in m^2, and usually m^3, of nearly all juvenals and many subadults. As a result of wear, the fold becomes reduced or completely erased in all adults of most series. In certain localities, however, a well-defined first primary fold persists in a large proportion of adults. The highest incidence of persistence appears in Arequipa (Arequipa; Yura; Balneario de Jesús), Moquegua (Torata at 9,400 and 11,200 feet), Tacna (below 12,800 feet), northern Chile (San Pedro; Ojos San Pedro; "Pocas") and in the *vaccarum* of Pearson (Paihuano). The incidence of persistence of a well-defined *pf* 1 in adult m^2 is lower in series of Pearson's *chilensis* from the Arequipa localities Cailloma, Salinas and Sumbay and the Chilean locality Putre. Persistence of the fold elsewhere within the broad range here assigned to *rupestris* is insignificant and sporadic. The data, taking into account juvenals, show a tendency for the character to persist in areas from the western portion of the range of *rupestris* southward through the range of *darwini*. Eastward across southern Peru, northern Chile and Bolivia, *pf* 1 in adult m^2 becomes weaker and virtually disappears at the eastern limits of the range. The character then suddenly reappears in adults of the bordering races *caprinus* and *wolffsohni*. It is significant that the highest incidence of occurrence of the first primary fold in $m^{2, 3}$ is in specimens sympatric with *magister* in which the same character is found. An analogous condition, already noted, is the frequent appearance of a pectoral streak among the *rupestris* sympatric with *Phyllotis osilae*.

Taxonomy.—*Mus rupestris* Gervais, originally described from the arid parts of Antofagasta, northern Chile, was determined by Osgood (1943, p. 205) as a pale race of *Phyllotis darwini*. The type of *Hesperomys lanatus* Philippi was examined by Osgood (op. cit., p. 208) in the National Museum of Santiago de Chile, and pronounced identical with *rupestris*. The same authority states that the types of the northern Chilean *Mus capito* Philippi and *Mus glirinus* Philippi are not now in the Santiago Museum but judged by the original descriptions, each may be regarded as a member of the common race. In the absence of evidence to the contrary, Osgood's conclusions are accepted.

The original description of *Phyllotis arenarius* Thomas agrees with that of *rupestris* as here defined. The type locality, Uyuni, Potosí, Bolivia, lies within the same faunal area as that of *rupestris*. Specimens at hand from Lipez, Bolivia, practically topotypes of *arenarius*, are not distinctive and were already assigned to *rupestris* by Osgood in 1943 (p. 206). Pearson (1958, p. 417) agreed.

Phyllotis darwini vaccarum Thomas, from Las Vacas (Punta Vacas), Mendoza, Argentina, judged by three topotypes at hand, should not be separated from Chilean *rupestris*. Osgood (loc. cit.) believed *vaccarum* differed from *rupestris* by its long tail and larger ears. Measurements were not given and none taken from the fresh skin are available for ears of specimens examined by Osgood. Tail lengths show no consistent difference. Osgood also distinguished *vaccarum* from typical *darwini* by its paler color. This character barely separates average *rupestris* from average *darwini*. Cutting this distinction finer for admitting another subspecies hardly improves the classification of these difficult rodents.

Pearson also recognized *vaccarum* but on the basis of size alone, the "head and body, skull and tooth row [being] longer than in *P. d. darwini*, *rupestris* and *ricardulus*." Pearson examined 127 specimens of *vaccarum* from nine widely distributed localities in Argentina and seven in Chile but gives measurements for only 10 to 18 specimens from four closely grouped Argentine localities (Punta Vacas, nearby Puente del Inca and not very distant Pedernal and Los Sombreros). Specimens from all other localities are treated by Pearson as intergrades between *vaccarum* and one or another of the other races mentioned. The type of *vaccarum*, collected in 1901 by P. O. Simons, deviated from Pearson's concept of the subspecies and was replaced by a "plesiotype" collected 20 years later by Budín. It appears that the "plesiotype" series of 21 specimens forms the chief if not the only basis for Pearson's characterization of *vaccarum*. This series and others from nearby localities average larger in size than Pearson's restricted *rupestris* but with such wide overlap in measurements that subspecific distinction is hardly indicated. Like northern *chilensis*, from which it is indistinguishable, *vaccarum* represents the opposite end of the gradient from *rupestris* to larger *posticalis* in the north and *xanthopygus* in the south.

Phyllotis ricardulus Thomas, described from Otro Cerro, Catamarca, Argentina, was distinguished from *vaccarum* by its "much smaller" ears. It was also compared with *wolffsohni* and *tucumanus* (=*P. osilae*). Pearson (1958, p. 418) characterized the type of *ricardulus* "as an example of the species *darwini* with large ears." He distinguished it from *rupestris* by its darker color, longer tail and larger molars and from *vaccarum* by smaller body, skull and tooth row. In effect *ricardulus* differs from *rupestris* by being more like *vaccarum* and from *vaccarum* by being more like *rupestris*. Clearly, *ricardulus* is nothing more than part of the cline leading from smaller *rupestris* to larger *vaccarum*.

Published measurements of the type of *Phyllotis oreigenus* Cabrera, from Laguna Blanca, Catamarca, and the figure of its upper molars with well-marked first primary folds point only to a juvenal of the common species. Persistence of a rudimentary mesoloph in the first and second upper molars of the type as described and figured by Cabrera, is also a character of sporadic occurrence in *P. darwini* or any phyllotine rodent, particularly the young. The measurement 13 mm. for zygomatic breadth of the type skull is right for a juvenal. Braincase width of 13.2 for the same skull, however, would be anomalous in *Phyllotis*. This last measurement must be either a typographical error or is faulty because of the damage to the occipital bone mentioned by Cabrera. Of four topotypes at hand, one is among the palest, the other among the darkest of all specimens here assigned to *rupestris*. Pearson (1958, p. 419) includes *oreigenus*, together with *wolffhuegeli*, in the synonymy of *vaccarum*.

The type specimen of *Phyllotis wolffhuegeli* Mann, from Bocatoma, Santiago, altitude 1800 meters, on the Chilean side of the Andes, is listed as an adult female in the introduction to the original description but identified as an immature male in the table of measurements in plate 9 of the original work. Accompanying figures of the skull of the type show the third molar recently erupted, a character of the suckling young in *Phyllotis*. All other characters said to be distinctive of *wolffhuegeli* are those distinguishing juvenal from adult *rupestris*.

Phyllotis osgoodi and *P. arenarius chilensis* Mann, both from Parinacota, Tarapacá, Chile, are juvenal and adult, respectively.

TABLE 23.—Measurements of *Phyllotis darwini rupestris* Gervais

Locality	Head and body	Tail	Hind foot	Weight	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
PERU								
Arequipa								
Yura ♂♂	108(98–125)18	117(94–128)18[1]	25(23–26)18		25(24–26)17	29.0(28.1–30.2)15	15.2(14.6–16.0)17	5.2(5.0–5.6)17
Yura ♀♀	105(103–115)6	111(104–123)6[2]	23.5(23–24)6		25(23–26)6	28.5(28.0–29.3)6	15.1(14.9–15.5)4	5.2(4.9–5.4)6
Yura[3]	85,100	101,93	24,23		24,24	26.9,26.0	14.3,13.9	4.9,4.9
Arequipa	99(89–111)13	112(94–129)12[4]	24(22–25)13	34(26–51)6	24.5(23–26)13	28.5(26.9–29.2)12	14.8(14.3–15.5)12	5.3(4.9–5.5)13
Jesus	118(110–126)7	118(110–126)7[5]	26.5(26–27)7		—	29.7(28.3–30.2)7	15.5(15.2–15.9)7	5.3(5.0–5.5)7
San Ignacio	114(105–124)5	126(120–136)5[6]	27(26–28)5		26(25–28)5	30.8(30.3–32.0)5	15.8(15.2–16.7)5	5.4(5.1–5.7)4
Cailloma	115(111–138)15	113(111–138)15[7]	28(25–30)15		26(23–30)14	30.3(29.1–32.3)13	15.7(15.0–16.5)14	5.4(4.7–5.8)16
Sibayo	103(96–116)5	117(109–124)5	27(26–28)5		26(24–27)5	30.5(29.3–31.0)5	15.3(14.9–15.8)5	5.2(5.0–5.7)5
Huaylarco	98,110,124,129	110,113,117,104	26,27,27,29	34,48,67,67	27,27,27,28	28.4,29.5,31.6,32.0	14.5,15.5,15.9,16.1	5.3,5.4,5.6,4.9
Imata	120	125	27	50	28	30.3	15.7	5.3
Sumbay	109(94–129)11	112(97–125)11[8]	27(25–29)11		26(24–27)8	29.8(28.2–30.8)9	15.2(14.6–15.7)10	5.2(5.0–5.6)11
Salinas	119(98–129)7	119(111–126)6[9]	25(24–27)7		26(24–29)7	30.1(27.7–31.0)7	15.1(14.4–15.5)6	5.3(5.0–5.5)7
Salinas	119,139	123,143	29,30	49,79	30,30	31.7,32.7	15.3,15.4	5.5,4.9
Moquegua								
Torata	97	115	23		23	28.5	15.2	5.0
Torata	103(91–123)6	114(105–124)6	24(22–25)6		25(23–27)6	29.1(28.0–30.7)6	15.0(14.4–15.7)6	5.2(5.0–5.3)6
Tala	96	114	26		22	28.1	14.0	4.9
Lago Viscacha	109	122	27		29	31.2	16.0	5.4
Lago Suche	99,111	110,112	25,27	36,61	25,28	28.4,31.7	14.9,16.1	5.0,5.0
Tacna								
Tarata, 11,500 ft.	99,94,103	113,111,102	23,23,23	35,42,39	24,23,24	27.7,28.0,28.6	14.3,14.4,14.4	4.9,5.0,5.2
Tarata, 12,200 ft.	101	107	23	39	26	30.0	15.1	5.4
Tarata, 12,800 ft.	113,112,128,123	118,118,119,114	25,26,27,27	52,42,—,—	26,26,26,28	29.5,29.9,30.2,31.6	15.0,15.0,16.1,16.4	5.5,5.4,5.5,5.6

TABLE 23. — Measurements of *Phyllotis darwini rupestris* Gervais (*continued*)

Locality	Head and body	Tail	Hind foot	Weight	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
Tarata, 13,000 ft.	97,116	102,120	25,27	39,37	24,28	—,29.9	—,15.2	5.2,5.1
Tarata, 13,200 ft.	116	110	27	58	26	30.1	15.1	5.0
Tarata, 13,500 ft.	105,117	114,125	28,26	33,44	25,26	28.2,29.3	—,15.4	5.2,5.6
Tarata, 14,600 ft.	106,111,112,111	107,111,92,118	25,25,25,26	43,51,56,52	26,25,25,27	28.8,29.2,30.7,31.5	14.9,14.6,15.8,15.3	5.0,5.0,5.3,5.4
Tarata, 15,200 ft.	107	106	27	47	25	29.7	15.3	5.0
Puno								
Asilla[10]	118	130	27	46	29	30.2	15.5	5.2
Asilla[10]	119(103–135)5	112(97–133)5[11]	29(28–30)5		—	31.1(28.0–32.3)5	15.1(14.1–16.2)5	5.2(5.0–5.6)5
Arapa[10]	112	112	26	38	27	28.9	—	5.3
Juliaca	91,104,107	109,128,110	27,26.5,27		24,24,24	28.5,31.0,31.0	14.6,15.7,15.8	5.4,5.3,5.9
Juliaca	123	119	29	55	26	31.0	16.1	5.4
Umayo[10]	110(103–118)4	109(103–112)4	26(25–27)4	41(36–48)4	25(24–27)4	29.4(28.2–30.9)4	15.2(14.7–15.8)4	5.1(4.8–5.4)4
Tincopalca	124	116	27		29	31.7	16.1	5.8
Puno, 82 km. W.	103,110	103,114	26,26		24, 27	28.0,30.6	14.7,15.6	5.3,5.4
Occomani[10]	,116	,116	—,23		—	30.3,31.7	15.5,16.0	5.3,5.7
Puno[10]	127(100–127)8	113(95–148)8	26(25–29)8	51(35–68)8	25(23–29)7	29.9(27.3–32.0)8	15.6(14.4–16.8)7	5.3(5.0–5.8)8
Chucuito[10]	119(104–139)7	108(96–121)7[12]	29(27–31)7		—	29.8(28.1–32.4)7	15.3(14.4–15.7)7	5.3(5.2–5.4)7
Ilave	114,107	92,110	26,27	54,53	26,28	30.7,31.4	15.7,15.8	5.7,5.4
Collacachi	122(115–127)5	118(110–131)5[13]	28(28–31)5		26(26–26)3	30.4(29.0–31.4)5	15.7(15.4–15.9)5	5.2(5.0–5.5)5
Esquilache	102,135	98,130	26,29		25,29	30.5,31.9	15.2,16.5	5.3,5.5
Juli[10]	96,104,105,109	97,116,122,123	25,26,27,25	—,—,45,45	27,23,26,25	28.8,28.9,29.3,29.7	15.2,15.4,15.8,15.2	5.5,4.8,5.4,5.6
Pomata[10]	105,131	115,119	25,26	36,64	26,26	28.1,31.2	15.0,16.2	5.2,5.3
Yunguyo[10]	146	134	30		—	—	16.4	5.7

TABLE 23.—Measurements of *Phyllotis darwini rupestris* Gervais (*continued*)

Locality	Head and body	Tail	Hind foot	Weight	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
Pairumani[10]	108,121,118	114,121,123	26,27,27	44,63,62	26,25,27	29.0,31.1,32.0	15.1,16.5,17.0	5.4,5.5,5.8
Huaculliani[10]	105,114,118,140	106,115,115,114	29,27,28,28		24,—,25,—	28.6,29.0,30.3,32.8	15.0,15.2,15.1,16.3	5.3,5.5,5.7,5.7
Santa Rosa	107(97–117)6	114(97–120)6	26.5(26–27)6		25(23–26)6	30.0(28.5–31.0)6	15.5(14.9–16.2)6	5.4(5.0–5.8)6
Santa Rosa[14]	94,99	100,105	25,25		24,24	27.4,27.9	14.1,15.3	5.2,5.0
Santa Rosa	116(109–133)5	111(105–122)5	28(25–30)5		25(24–26)5	30.6(29.3–31.7)5	15.3(15.0–15.5)5	5.4(5.3–5.5)5
Caccachara	110(104–124)9	107(96–117)9	26(24–28)9		26(24–28)9	29.5(28.2–30.5)9	15.4(15.1–16.0)9	5.4(5.2–5.7)9
Mazocruz	98	105	24	36	26	28.7	14.7	5.1
Pisacoma	118,129	107,114	28,29		—	29.0,30.9	14.4,15.9	5.1,5.4
Ancomarca	100,110,127	112,117,114	27,26,27	37,46,69	23,25,26	27.3,31.0,28.5	14.9,14.7,16.4	4.9,5.3,5.4
CHILE								
Parinacota[15]	84	96	24		19.6	25.2	13.2	4
Parinacota[16]	117	83	27		28	30.6,(29.5)	15.3(14.6)	5.7(4.5)
Putre	115,111,109	113,90,103	25,27,26		—	28.7,28.8,29.7	14.5,14.1,14.3	5.2,5.3,5.5
Caritaya	110(104–117)6	117(111–128)6	26(25–27)6	44(35–52)6	26(25–27)6	29.2(28.0–29.9)4	15.2,15.3,15.5	5.2(4.9–5.5)6
Ojos de San Pedro	115(104–124)4	105(97–113)4	27.5(27–28)4	45(32–61)4	25(23–27)4	29.8(27.7–31.0)4	15.2(14.0–15.8)4	5.6(5.1–5.9)4
San Pedro	113(103–134)10	105(89–125)10[17]	27(26–30)10		—	30.0(29.0–32.4)9	15.4(14.7–16.5)9	5.2(5.0–5.3)9
San Pedro[18]	151	107	24		—	—	—	—
San Pedro[19]	141	95	25		19.5	31.0	—	5.3
San Pedro[20]	94	118	25		—	26.7	14.2	4.5
Hueso Parado[21]	85	74	22		—	—	—	—

TABLE 23.—Measurements of *Phyllotis darwini rupestris* Gervais (*continued*)

Locality	Head and body	Tail	Hind foot	Weight	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
Toconce	118,112,113	130,103,118	25,26,25	43,48,50	25,25,26	28.3,29.4,29.5	14.7,14.8,15.0	4.8,5.0,4.8
Tatio Geysers	119	117	26	51	24	30.3	15.2	5.3
Domeyko	124,128	116,117	27,28		—	31.3,33.2	16.3,17.0	5.4,5.4
Baños	127,120	126,92	28,27		—	31.3,31.7	16.2,—	5.8,5.6
Paiguano ♂♂	123(111–138)16	127(116–140)15[22]	29(28–31)16		—	30.2(29.5–31.2)16	15.4(14.8–15.8)16	5.2(4.8–5.5)16
Paiguano ♀♀	112(99–127)9	122(112–135)9[23]	28(27–29)9		—	29.9(28.6–31.2)8	15.0(14.5–16.2)9	5.2(4.9–5.5)9
Bocatoma[24]	89	86	23		20	—	—	—
Río Maule	134,144,153	108,130,125	30,32,32		—	—,34.1,—	—	6.1,6.3,6.7
BOLIVIA								
La Paz	99(94–104)4	117(109–133)4	25(24–27)4		25(23–26)4	29.0(27.5–30.3)4	14.8(14.0–15.5)4	5.2(5.0–5.4)4
Oruro	95,95	104,109	24,25		24,25	27.7,28.3	14.4,14.9	5.0,5.0
Potosí	99(85–109)6	110.3(98–119)6	25(24–27)6	31(27–36)5	24.5(24–25)6	28.0(26.7–29.2)6	14.5(13.9–14.8)6	5.2(5.2–5.3)6
Uyuni[25]	118	114	27		26	30	14.5	4.9
Uyuni	98(91–108)9	108(98–117)9	24(23–26)9	32(22–38)9	24(23–25)9	27.9(26.5–29.3)9	14.5(13.7–15.2)9	4.9(4.7–5.2)9
Camataquí	104(97–113)7	118(108–129)7	25(24–26)8		24(24–26)8	28.3(27.5–29.0)8	14.7(14.2–15.2)8	5.2(4.8–5.8)8
Lipez	111,111,119	116,126,—	24,25,25		23,25,26	28.4,29.3,30.3	15.2,15.2,15.5	5.4,5.0,5.0
Villazón	102(96–107)4	110(106–114)4	24.5(24–25)4		24(24–25)4	27.8(27.3–28.3)4	14.7(14.3–15.3)4	5.1(5.0–5.3)4
Perez	108(100–115)10	117(105–125)10[26]	25(25–28)10		24(22–25)10	29.4(28.6–30.7)8	14.9(14.4–15.5)8	4.7(4.5–5.1)10
Pacajes	105,105,115	125,135,155	25,25,30		25,25,25	29.5,29.6,—	15.5,—,15.2	5.7,5.5,4.9
Sajama	90,95	105,125	25,25		25,25	28.2,28.3	14.4,14.6	4.6,5.0
ARGENTINA								
Tres Cruces	99,118	121,118	25,23		22,25	29.1,29.8	—,15.4	5.0,5.5
Tilcara	101(91–108)7	110(105–117)7	25(24–26)7		25(23–26)7	27.8(26.1–29.0)7	14.3(13.9–14.8)7	5.1(4.7–5.5)7
Otro Cerro	112	145	26		—	30.0	15.8	5

TABLE 23.—Measurements of *Phyllotis darwini rupestris* Gervais (*concluded*)

Locality	Head and body	Tail	Hind foot	Weight	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
Chumbicha	115,123	—,123	25,25		21,22	29.4,30.2	—,15.3	5.2,5.0
San Antonio	122	114	24		24	29.2	—	5.3
G. M. Sola	135	129	26		25	32.2	16.3	5.6
Puesto Viejo	—	—	—		—	31.0	—	—
Laguna Blanca[27]	88	99	24.8		18[sic]	—	13	5.2
Laguna Blanca	129,131,120	142,125,120	27,28,25.5		—	32.5,32.8,—	16.8,16.5,16.5	5.7,6.2
Otro Cerro[28]	112	145	26		—	30.5	15.8	5
Sombreros	125	130	26		27	—	—	5.7
Punta Vaca[29]	130	140	28		27	31.7	17.5	5.8
Punta Vaca[30]	106,119	116,128	26,27		—	29.4,29.7	—,—	5.5,5.5
Puente Inca	135,127,135	116,130,—	28,29,28		—	32.3,32.6,33.0	15.7,16.2,16.1	6.0,6.0,6.5
Chos Malal	103,116	101,130	27,30		24,29	28.2,30.5	—,15.8	5.7,5.8
Collon Cura[30]	128	118	29		25	28.6	—	5.2

[1] Tails of 13 longer, 2 equal, 3 shorter than combined head and body length. Tail: head and body = (89–131):100; average, 110%.

[2] Tails of 4 longer, of 2 shorter than combined head and body length. Tail: head and body = (97–121):100; average, 107%.

[3] Probably juvenals (CNHM 49463 ♀, 49474 ♀) but appear to be dwarfed adults; pelage and color as in adults, crania fully ossified, molars worn but first primary fold of m^2 persistent.

[4] Tails of all longer than combined head and body length. Tail: head and body = (102–124):100; average, 113%.

[5] Tails of 3 longer, 2 equal, 2 shorter than combined head and body length. Tail: head and body = (96–109):100; average, 102%.

[6] Tails of 4 longer, 1 shorter than combined head and body length. Tail: head and body (95–124):100; average, 111%.

[7] Tails of 9 longer, 1 equal, 5 shorter than combined head and body length. Tail: head and body = (93–128):100; average, 106%.

[8] Tails of 6 longer, 5 shorter than combined head and body length. Tail: head and body = (92–125):100; average, 106%.

[9] Tails of 3 longer, 3 shorter than combined head and body length. Tail: head and body = (93–120); average, 103%.

[10] See Table 30, p. 357, for additional measurements and comparisons with sympatric series of *Phyllotis osilae*.

[11] Tails of all shorter than combined head and body length. Tail: head and body = (87–98):100; average, 93%.

[12] Tails of all shorter than combined head and body length. Tail: head and body = (87–96):100; average, 91%.

[13] Tails of 1 longer, 1 equal, 3 shorter than combined head and body length. Tail: head and body = (91–106); average, 97%.

[14] Dwarfs? molars worn.

[15] Type of *osgoodi* Mann; measurements from original description.

[16] Type of *chilensis* Mann; measurements in parentheses from original description.

[17] Tails of 4 longer, 6 shorter than combined head and body length. Tail: head and body = (75–103):100; average, 93%.

[18] Type of *glirinus* Philippi; measurements from original description.

[19] Type of *lanatus* Philippi; measurements of head and body, tail and hind foot, from original description, of ear (dry), skull and molars from Osgood (1943, p. 208).

[20] Dwarf.

[21] Type of *capito* Philippi; measurements from original description.

[22] Tails of 9 longer, 1 equal, 5 shorter than combined head and body length. Tail: head and body = (84–124):100; average, 104%.

[23] Tails of 6 longer, 1 equal, 2 shorter than combined head and body length. Tail: head and body = (97–128):100; average, 108%.

[24] Type of *wolffhuegeli* Mann, a juvenal; measurements from original description.

[25] Type of *arenarius* Thomas; measurements from original description.

[26] Tails of 9 longer, 1 shorter than combined head and body length. Tail: head and body = (100–115):100; average, 108%.

[27] Type of *oreigenus* Cabrera; measurements from original description.

[28] Type of *ricardulus* Thomas; measurements from original description.

[29] Type of *vaccarum* Thomas; measurements from original description.

[30] Subadults.

of *Phyllotis darwini rupestris*. Pearson, however, recognized *chilensis* (with the prior name *osgoodi* a synonym) as a valid subspecies of *darwini* "intermediate in size of most parts and in color between *posticalis* and *rupestris*." Inasmuch as most populations are also geographically intermediate and others wholly encompassed by or cutting completely across the range of *rupestris*, Pearson's *chilensis* may be better described as a heterogeneous combination of intergrading populations between *posticalis* and northern *rupestris* and between eastern *rupestris* and western *rupestris* and isolated peak populations wholly derived from *rupestris* stock. Moquegua and Tacna *chilensis* of Pearson average slightly darker than most *rupestris* to the east and west but are hardly if at all distinguishable from northern Chilean specimens (Ojos de San Pedro; San Pedro; Tatio Geysers) regarded by Pearson (1958, p. 417) as typical *rupestris*. Pearson (1958, p. 416) himself experienced difficulty in attaching "the name *chilensis* to a subspecies that ranges primarily in southern Peru [and with a] type specimen [which] is not typical of the subspecies." Actually, the type of *chilensis* is indistinguishable from typical representatives of *rupestris*. If a southern Peruvian race of *darwini* were indeed recognizable, the name *chilensis* could not be used for it.

Forty specimens from Paposa, Antofagasta, and two from Vallenar, Atacama, included with *darwini* by Pearson (1958, p. 421), were described by him as "pale-colored but relatively large-eared," and considered "to be intergrades with *rupestris* and *vaccarum*." I have not seen the Paposa and Vallenar specimens but their geographic distribution, color and size, as described, point to the small, pale *rupestris* rather than the larger, warmly colored *darwini*. Specimens of similar color and size from localities in the same area (Domeyko, Atacama; "east of Taltal," Antofagasta) are identified as *rupestris* by Pearson and in this paper. No published measurements are available for the Vallenar specimens but for the Paposa series Pearson (1958, Appendix I) includes head and body 105 (90–125, 26 specimens), ears 26 (19–30, 28 specimens). These compare with the following of *darwini* from "Santiago, Valparaiso and Aconcagua," according to the same authority: head and body 120 (107–140, 29 specimens), ear 25.9 (21–32). Relative to head and body, the ears of the Paposa series average appreciably larger than those of central Chilean *darwini*. On the other hand, they can be more nearly matched in size with ears of a number of populations of *rupestris* (including *vaccarum*) scattered throughout the range of the subspecies (cf. Table 23). Actually, ear measurements of fresh material and visual comparisons of ears in dry skins show considerable variation and give little or no basis for determination of the systematic position of any one population of *rupestris* or of *darwini*. The foregoing geographical and zoological considerations indicate the assignment of the Paposa and Vallenar series to *rupestris*, not *darwini*. It is noted that Pearson excludes Antofagasta and Atacama from the range of *P. d. darwini*.

Remarks.—At several points along the periphery of its range in southwestern Peru, *Phyllotis darwini rupestris* contacts but, presumably, does not interbreed with, *P. d. magister*. On the northeastern border of its range, in Puno, Peru, and, probably, in La Paz, northern Bolivia, *rupestris* lives side by side with representatives of the strikingly similar *Phyllotis osilae*. The ranges of *rupestris* and *P. osilae* continue southward through the Andes of Bolivia and northern Argentina, their common borders overlapping or interdigitating at several points. In some parts of the same sections of Bolivia and Argentina *P. darwini caprinus* appears. Whether or not *caprinus* actually contacts *rupestris* is moot. Observations made by Pearson indicate that the two may occur in the same general area but are ecologically segregated. For further discussions on the relationship of *rupestris* to *caprinus* and other forms, see the corresponding species and subspecies accounts.

Measurements.—See Table 23.

Specimens examined.—473. ARGENTINA. *Catamarca:* Chumbicha, 2 (CNHM); Laguna Blanca, 4 (CNHM, 2; MACN, 2). *Jujuy:* La Laguna, Sierra de Zenta, 2 (CNHM, 1; MACN, 1); Tilcara, 1 (AMNH); Tilcara, ½ mi. E, 7 (MVZ); Tres Cruces, 2 (CNHM). *La Rioja:* Puesto Viejo, 1 (MACN). *Los Andes:* San Antonio de los Cobres, 4 (CNHM, 1; MACN, 3). *Mendoza:* Puente del Inca, 4 (AMNH); Punta Vaca, 3 (CNHM). *Neuquén:* Chos Malal, 2 (CNHM); Collon Cura, 1 (CNHM). *Salta:* G. M. Sola, 2 (CNHM). *San Juan:* Angaco Sud, 1 (AMNH); Los Sombreros, 1 (CNHM). BOLIVIA. *Cochabamba:* Tin Tin, 1 (CNHM). *La Paz:* Esperanza, 3 (CNHM); Estación Perez, 11 (CNHM); La Paz, 20 mi. S, 4 (MVZ). *Oruro:* Oruro, 40 mi. S, 2 (MVZ); Sajama (Mt.), 3 (CNHM). *Potosí:* Lipez, 3 (CNHM); Potosí, 20 mi. S, 6 (MVZ); Uyuni, 10 (MVZ); Villazón, 6 (MVZ). *Tarija:* Camataquí, 8 (MVZ). CHILE. *Antofagasta:* Muelle de Piedra, E of Taltal, 1 (AMNH); Ojos de San Pedro, 4 (MVZ); Pocos, 1 (MVZ); San Pedro, 16 (CNHM); Tatio Geysers, 1 (MVZ); Toconce, 3 (MVZ). *Atacama:*

Domeyko, 2 (CNHM). *Coquimbo:* Baños del Toro, 2 (CNHM); Paiguano, 43 (CNHM, 41; USNM, 2). *Santiago:* Los Valdes, 5 (USNM, including type of *wolffhuegeli* Mann); Río Blanco, 1 (USNM). *Talca:* Arroyo del Valle, 1 (CNHM); Río Maule, 4 (CNHM). *Tarapacá:* Caritaya, 6 (MVZ); Parinacota, 1 (USNM, type of *chilensis* Mann); Putre, 8 (CNHM); Timar, 1 (USNM). PERU.—*Arequipa:* Arequipa, 2 (CNHM); Arequipa, 7 km. E, 7 (MVZ); Arequipa, 12 km. SSW, 4 (MVZ); Balneario de Jesus, 13 (CNHM); Ongoro, Valle de Mages, 2 (CNHM); Yura, 29 (CNHM); Cailloma, 26 (CNHM); Huaylarco, 5 (MVZ); Imata, 3 (MVZ); Salinas, 13 (CNHM, 11; MVZ, 2); San Ignacio, 5 (MCZ); Sibayo, 7 (MCZ); Sumbay, 14 (CNHM). *Moquegua:* Río Torata, 15 km. NE Torata, 6 (MVZ); Torata, 10 km. NE, 2 (MVZ); Tala, 2 (MVZ); Lago Viscacha, 1 (MVZ); Lago Suche, 3 (MVZ). *Tacna:* Tarata, 2 km. N, 4 (MVZ); Tarata, 3 km. N, 2 (MVZ); Tarata, 4 km. N, 5 (MVZ); Tarata, 4.5 km. N, 2 (MVZ); Tarata, 5 km. N, 2 (MVZ); Tarata, 20 km. NE, 5 (MVZ); Tarata, 25 km. NE, 1 (MVZ); Tarata, 8 mi. NE, 2 (MVZ). *Puno:* Arapa, 1 (MVZ); Asilla, 6 (CNHM, 5; MVZ, 1); Caccachara, 12 (MCZ, 11; MVZ, 1); Collacachi, 11 (CNHM); Chucuito, 8 (CNHM); Huacullani, 4 (CNHM); Ilave, 3 (MVZ); Juli, 11 (MCZ, 6; MVZ, 5); Juliaca, 4 (CNHM, 3; MVZ, 1); Mazocruz, 30 mi. S, 1 (MVZ); Occomani, 2 (CNHM); Pairumani, 3 (MVZ); Pampa de Ancomarca, 3 (MVZ); Pisacoma, 4 (CNHM); Pomata, 2 (MVZ); Puno, 8 (CNHM, 1; MVZ, 7); Puno, 82 km. W, 2 (MVZ); Río Santa Rosa, 3 (MVZ); San Antonio de Esquilache, 2 (CNHM); Santa Rosa de Juli, 13 (MVZ); Santa Rosa, 2 mi. W, 2 (MVZ); Sorapa, 2 (AMNH); Tincopalca, 1 (MVZ); Umayo, 4 (MVZ); Yunguyo, 3 (CNHM).

Phyllotis darwini darwini Waterhouse

Mus (*Phyllotis*) *Darwinii* Waterhouse, 1837, Proc. Zool. Soc. London, **1837:** 28.

Mus Darwinii, Waterhouse, 1839, Zool. Voy. "Beagle," Mammalia, p. 64, pl. 23 (animal), pl. 34, fig. 17 (molars)—*Coquimbo* (Coquimbo). Gay, 1847, Hist. Chile, Zool., **1:** 117.

H[*esperomys*] *darwini*, Thomas, 1884, Proc. Zool. Soc. London, **1884:** 449—type of subgenus *Phyllotis*.

Phyllotis darwinii, Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9:** 131—*Valparaiso* (Valparaiso).

Phyllotis Darwini, Cabrera, 1905, Rev. Chilena Hist. Nat., **9:** 16—part, *Valparaiso* (Quillota).

Phyllotis darwini, Wolffsohn and Porter, 1908, Rev. Chilena Hist. Nat., **12**: 79—*Valparaiso* (Valparaiso); *Mus capito* Philippi, a synonym. Thomas, 1927, Ann. Mag. Nat. Hist., (9), **19**: 556—*Santiago* (Puente Alto, southeast of Santiago).

Phyllotis darwini darwini, Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 200—taxonomy; characters; distribution; *Aconcagua* (La Ligua; Longotoma; Los Agostinos, Palomar; Papudo); *Coquimbo* (Romero); *Santiago* (San Cristóbal); *Valparaiso* (Buen Retiro, Las Hijuelas; Las Rojas, Quillota; Olmue; Palmilla, La Cruz). Pearson, 1958, Univ. California Publ. Zool., **56**: 421—taxonomic revision; distribution (for locality records see p. 250).

Mus melanonotus Philippi *in* Philippi and Landbeck, 1858, Arch. Naturg., (24), **1**: 78—type locality, near Angostura, Santiago. Philippi, 1900, Anal. Mus. Nac. Chile, Zool., Entr., **14a**: 43, pl. 18, fig. 1 (animal)—type specimen lost.

Mus dichrous Philippi, 1900, Anal. Mus. Nac. Chile, Zool., Entr., **14a**: 14, pl. 3, fig. 2 (animal)—type locality, "Provincia Santiago, prope Peine." Wolffsohn, 1910, Bol. Mus. Nac. Chile, **2**: 88—*dichrous*=*Phyllotis darwini* juv.

Mus megalotis Philippi, 1900, Anal. Mus. Nac. Chile, Zool., Entr., **14a**: 15, pl. 3, fig. 3 (animal)—type locality, "provincia Santiago."

Mus mollis Philippi, 1900, Anal. Mus. Nac. Chile, Zool., Entr., **14a**: 23, pl. 7, fig. 1 (animal)—type locality, "provincia Santiago." Wolffsohn, 1910, Bol. Mus. Nac. Chile, **2**: 90—*mollis*=*Phyllotis darwini*.

Mus illapelinus Philippi, 1900, Anal. Mus. Nac. Chile, Zool., Entr., **14a**: 28, pl. 9, fig. 1 (animal)—type locality, near Illapel, Coquimbo. Wolffsohn, 1910, Bol. Mus. Nac. Chile, **2**: 93—*illapelinus*=*Phyllotis darwini*.

Mus Segethi Philippi, 1900, Anal. Mus. Nac. Chile, Zool., Entr., **14a**: 30, pl. 11, fig. 2 (animal)—type locality, "planitie provinciae Santiago loco dicto Peine." Wolffsohn, 1910, Bull. Mus. Nac. Chile, **2**: 94—*segethi*=*Phyllotis darwini*.

Mus campestris Philippi, 1900, Anal. Mus. Nac. Chile, Zool., Entr., **14a**: 38, pl. 16, fig. 1 (animal)—type locality, Choapa, Coquimbo. Wolffsohn, 1910, Bol. Mus. Nac. Chile, **2**: 98—*campestris*=*Phyllotis darwini*.

Mus melanotis Philippi, 1900, Anal. Mus. Nac. Chile, Zool., Entr., **14a**: 39, pl. 16, fig. 3 (animal)—type locality, none given but certainly in Chile.

Mus platytarsus Philippi, 1900, Anal. Mus. Nac. Chile, Zool., Entr., **14a**: 47, pl. 19, fig. 4 (animal)—type locality, La Ligua, Aconcagua.

Mus boedeckeri Philippi, 1900, Anal. Mus. Nac. Chile, Zool., Entr., **14a**: 53, pl. 22, fig. 2 (animal)—type locality, Coroney Ranch, near Quirihue, Nuble, Chile.

Phyllotis darwini boedeckeri, Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 202—characters; *Maule* (Pilen Alto); *Nuble* (Quirihue). Pearson, 1958, Univ. California Publ. Zool., **56**: 422—review.

Mus griseoflavus Philippi, 1900, Anal. Mus. Nac. Chile, Zool., Entr., **14a**: 55, pl. 24, fig. 1 (animal)—type locality, near La Serena, Coquimbo; name preoccupied by *Mus griseoflavus* Waterhouse, 1837. Wolffsohn, 1910, Bol. Mus. Nac. Chile, **2**: 99—*griseoflavus* Philippi=*Phyllotis darwini*.

P[*hyllotis*] *darwini vaccarum*, Wolffsohn (not Thomas), 1921, Rev. Chilena Hist. Nat., **25**: 517—*Aconcagua* (Alcahue, San Felipe).

Type.—Adult, British Museum (Natural History) no. 55.12. 24.183; collected May 1835, by Charles Darwin.

Type locality.—Coquimbo, Coquimbo, coast of central Chile.

Distribution (figs. 70, 75).—Coastal plains and hills of central Chile from the vicinity of Coquimbo southward into the province of Maule and, possibly, continuing as far as the Río Bío Bío in Concepción; altitudinal range from sea level to approximately 1000 meters above.

Specimens from Paposa, Antofagasta, and Vallenar, Atacama, described by Pearson (1958, p. 421) as intergrades between *darwini* and *rupestris* (and *vaccarum*) are included with *rupestris* in this paper (cf. p. 318).

Characters.—Larger than Peruvian, Bolivian and northern Chilean *rupestris* but smaller than Argentine and central Chilean *rupestris* (*vaccarum*); more warmly colored, more ochraceous on upper parts and sides than *rupestris*, paler throughout, particularly on underparts, than *fulvescens;* pale underparts thinly washed with buff or ochraceous; pectoral streak often present; ears apparently large; tail bicolor, comparatively thinly haired with pencil poorly developed, length more or less than head and body combined, average, 98.5 per cent (84–116 per cent, 34 specimens); auditory bullae comparatively well inflated, their antero-posterior length, less tubes, about 5.4 (4.9–5.9, 34 specimens) and subequal to alveolar length of molar row; bullar tubes short to moderately elongate; mesopterygoid fossa measured at base of hamular processes usually narrower, sometimes as wide as, parapterygoid fossa; hamular processes usually divergent; posterior border of palate rounded or notched, or with a pair of minute processes which sometimes fuse into a single median spine; postero-lateral palatal pits anteriad to posterior border of palate in all specimens examined; interorbital region generally narrow, the edges square or pinched upward; fronto-parietal sutures rounded not V-shaped; proximal ends of nasals truncate or pointed and terminating slightly in front of to slightly behind fronto-maxillary suture; alveolar length of molar row, 5.4 (5.0–5.9, 35 specimens).

Variation.—Juvenals and subadults are more gray, less ochraceous, than adults and resemble adult *rupestris*. Individuals from lower elevations are more warmly colored than those from higher altitudes. Five specimens, none adult, from Romero, on the coast north of Coquimbo, are virtually topotypes. They are more brightly colored, more ochraceous, than neighboring representatives of *rupestris* from Paihuano, to the east in the cordilleras and from Domeyko in the desert to the north.

The skull of an adult from Quilpué, Valparaiso (AMNH 33269), with zygomata unusually expanded, resembles, in dorsal view, a miniature skull of *Chinchillula* or *Andinomys*. An abnormal skull of a young individual from Palmilla, Aconcagua (CNHM 23880), is flattened in dorsal contour, its nasals extremely short, not reaching anteriorly to tips of premaxillaries, and the anterior half of its palate is plane, not slightly concave as in normal crania. The rugosities of the frontal bones, especially along sutures and the non-inflated frontal sinuses, suggest a traumatic origin of the abnormalities (fig. 80, *b*).

Taxonomy.—After having based no less than 14 names, all synonyms of *Phyllotis darwini* (sensu lato), on specimens in the Santiago de Chile Museum, Philippi (Anal. Mus. Nac. Chile, Entr.,**14a**:11) complained that the museum still lacked a representative of the species. Three of the 14 names proposed by Philippi are referable to *P. d. rupestris* (*q.v.*). The types, or bona fide representatives, of ten of the named forms were examined by Wolffsohn and by Osgood, and referred by each to typical *darwini*. The fourteenth, *Mus boedeckeri* Philippi, was recognized by Osgood as a valid subspecies "smaller and shorter-tailed" than typical *darwini*. The type of *boedeckeri*, judged by measurements, is immature. Of the three specimens from the province of Maule, examined by Osgood, one from Pilen Alto is a juvenal, and two from Quirihue are young adults. Their body size and relative tail lengths lie within the range of variation of comparably aged individuals of true *darwini*.

Remarks.—The types of Philippi's *Mus dichrous* and *M. segethi* are said to be from near Peine, Santiago. Osgood (1943, p. 200) cites it as "Peine, O'Higgins." I find a Paine but no Peine in Santiago and none in O'Higgins or any other province within the geographic range of the subspecies. For present purposes, Paine, Santiago, is regarded as the type locality of both *dichrous* and *segethi*.

Measurements.—See Table 24.

Specimens examined.—41. CHILE. *Aconcagua:* Buen Retiro, 5 (CNHM); Longotoma, 1 (CNHM); Los Agostinos, 1 (CNHM); Papudo, 11 (CNHM, 10; MCZ, 1). *Coquimbo:* Romero, 5 (CNHM). *Maule:* Pilen Alto, 1 (CNHM). *Nuble:* Quirihue, 2 (CNHM).

Table 24. —Measurements of *Phyllotis darwini darwini* Waterhouse

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
CHILE							
Coquimbo[1]	152	120	28.6	—	—	—	5.0
Romero[2]	122,122	115,126	29,30	—	30.2,30.5	15.4	5.2,5.4
La Serena[3]	110	90	25	—	—	—	—
Illapel[4]	178[?]	114	—	—	—	—	—
Choapa[5]	128	100	28[s.u.]	—	—	—	—
La Calera	—,130	—,—	23,30	—	31.8,32.1	—,17.1	—,5.5
Buen Retiro	124,131,140	124,123,124	29,26,28	—	31.0,32.0,32.9	16.1,16.9,16.3	5.7,5.6,5.4
La Ligua[6]	127	105	28	—	—	—	—
Papudo	136(117–160)7	126(116–137)7	29(26–32)7	—	31.6(29.6–34.8)6	16.3(15.5–17.7)7	5.5(5.3–5.7)7
Agostinos	129	126	27	—	31.2	15.6	5.7
Las Rojas	127	110	30	—	31.1	16.5	5.2
Quilpué	120	—	26	26	32.8	18.0	5.9
S. Cristóbal	115,120	105,120	30,25	25,25	30.2,33.4	14.9,16.6	5.3,5.4
Angostura[7]	139	112	26	—	—	—	—
Santiago Prov.[8]	112	90	29	—	—	—	—
Santiago Prov.[9]	132	94	25	—	—	—	—
"Peine"[10]	115	69	25	—	—	—	—
"Peine"[11]	146	122	25	—	—	—	—
Quirihue	116	104	27	—	29.8,30.7	15.3,15.8	5.5,5.3
Coroney[12]	95	102	26	—	—	—	—
No locality[13]	145	77	22	—	—	—	—

[1] Type of *darwini* Waterhouse; external measurements from original description; molar row measurement from Gyldenstolpe (1932, p. 144).

[2] Subadults. [3] Type of *griseoflavus* Philippi; measurements from original description.

[4] Type of *illapelinus* Philippi; measurements from original description.

[5] Type of *campestris* Philippi; measurements from original description.

[6] Type of *platytarsus* Philippi; measurements from original description.

[7] Type of *melanonotus* Philippi; measurements from original description.

[8] Type of *megalotis* Philippi; measurements from original description.

[9] Type of *mollis* Philippi; measurements from original description.

[10] Type of *dichrous* Philippi; measurements from original description.

[11] Type of *segethi* Philippi; measurements from original description.

[12] Type of *boedeckeri* Philippi; measurements from original description.

[13] Type of *melanotus* Philippi; measurements from original description.

Santiago: San Cristóbal, Santiago, 2 (CNHM). *Valparaiso:* La Calera, 2 (CNHM, 1; MCZ, 1); Las Rojas, 2 (CNHM); Olmue, 4 (CNHM); Palmilla, La Cruz, 2 (CNHM); Quilpué, 3 (AMNH, 2; MCZ, 1).

Phyllotis darwini fulvescens Osgood

Phyllotis darwini fulvescens Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 204. Pearson, 1958, Univ. California Publ. Zool., **56**: 422—review.

Type.—Adult female, Chicago Natural History Museum no. 50550; collected 8 November, 1939, by Wilfred H. Osgood.

Type locality.—Piedra de Aiguilas [Aguilas?] near summit of Sierra Nahuelbuta, west of Angol, Malleco, Chile; altitude, 1250 meters.

Distribution (figs. 70, 75).—Known only from the Araucaria forest in the Sierra de Nahuelbuta, Malleco, Chile.

Characters.—Most warmly colored race of *Phyllotis darwini;* size approximately as in the nominate subspecies or perhaps smaller; back warm brown, underparts heavily washed ochraceous, with dark basal portion of hairs showing through; ochraceous lateral line broad and well defined; tail thinly haired, short (85 per cent [type], 92 per cent of head and body length) and bicolor except brown tip; cranial characters generally as in *darwini;* interorbital region narrow, the sides pinched upward; proximal ends of nasals pointed and terminating slightly behind fronto-maxillary suture; the median nasal sulcus unusually deep; molar row 5.9 (2 specimens).

Remarks.—*Phyllotis darwini fulvescens* and *P. osilae phaeus* are the darkest members of the *Phyllotis darwini* group. Each form inhabits a region of high rainfall.

The subspecies is represented only by the type and a very similar specimen from the same general region collected 6 January, 1930, by H. E. Anthony and G. Ottley. The subspecies is most nearly approached in color by an extremely dark series of *P. d. xanthopygus* from Laguna Lazo, Magallanes, Chile. The latter, however, is much larger, with hairy tail and lateral line subdued. The geographically nearer populations of *darwini* from Quirihue and Pilen Alto, are distinctly paler with smaller molars.

Measurements.—See Table 25.

Specimens examined.—2. CHILE.—*Malleco:* Sierra Nahuelbuta, 1 (CNHM, the type); Araucaria Forest, Nahuelbuta, 1 (AMNH).

Table 25.—Measurements of *Phyllotis darwini fulvescens* Osgood

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
Nahuelbuta[1]	123	104	27	—	30.1 (ca.)	16.3	5.9
Nahuelbuta	128	118	28	—	—	16.5	5.9

[1] Type of *fulvescens;* skull damaged with most of occipital region missing.

Phyllotis darwini xanthopygus Waterhouse

Mus (*Phyllotis*) *xanthopygus* Waterhouse, 1837, Proc. Zool. Soc. London, **1837**: 28. Thomas, 1919, Ann. Mag. Nat. Hist., (9), **3**: 202—type a true *Phyllotis*.

Mus xanthopygus, Waterhouse, 1839, Zool. Voy. "Beagle," Mammalia, pt. 2, p. 63, pl. 22 (animal), pl. 34, fig. 16 (molars)—ARGENTINA: *Santa Cruz* (Port Desire; Santa Cruz).

Hesperomys xanthopygus, Burmeister, 1879, Descr. Phys. Rep. Argentina, **3**: 225—ARGENTINA: *Santa Cruz* (Río Santa Cruz). Burmeister, 1891, Anal. Mus. Nac. Buenos Aires, **3**: 314—ARGENTINA: *Santa Cruz* (Caprek-aik).

H[*esperomys*] *xanthopygus*, Thomas, 1884, Proc. Zool. Soc. London, **1884**: 449—subgenus *Phyllotis*.

[*Hesperomys* (*Phyllotis*)] *xanthopygos* [sic], Trouessart, 1880, Bull. Soc. Etudes Scient., Angers, **1880**, (1): 135—classification.

Hesperomys (*Phyllotis*) *xanthopygus*, Thomas, 1891, in Milne-Edwards, Mission du Cap, **6**: Mamm, p. A. 29, pl. 6, fig. 2 (animal)—ARGENTINA: *Santa Cruz* (Santa Cruz).

Euneomys (*Auliscomys*) *xanthopygus*, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 143—classification.

[*Phyllotis*] *xanthopygus*, Trouessart, 1897, Cat. Mamm., p. 534—classification.

Phyllotis xanthopygus, Allen, 1905, Princeton Univ. Exped. Patagonia, **3**, (1), Mamm., p. 58, pl. 13, fig. 1 (skull), pl. 14, figs. 2, 3 (molars)—ARGENTINA: *Santa Cruz* (Río Chico; Swan Lake; Basaltic Canyons). Thomas, 1919, Ann. Mag. Nat. Hist., (9), **3**: 200—ARGENTINA: *Río Negro* (Pilcaniyeu). Thomas, 1919, op. cit., (9), **3**: 202—true *Phyllotis*, not *Euneomys* as classified in 1916. Thomas, 1927, op. cit., (9), **19**: 549—lectotype, British Museum (Natural History) no. 55.12.24.185, from Santa Cruz, Patagonia, lectoparatype from Port Desire. Yepes, 1935, Anal. Mus. argentino Cienc. Nat., **38**: 335—ARGENTINA: *Chubut* (Río Senguer).

Phyllotis darwini xanthopygus, Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 208—part, ARGENTINA: *Chubut* (Tecka), *Río Negro* (Huanuluán; Pilcañeu); CHILE: *Magallanes* (Laguna Lazo, near Lago Sarmiento). Pearson, 1958, Univ. California Publ. Zool., **56**: 420—part, ARGENTINA: *Chubut* (Pico Salamanca; Tecka), *Río Negro* (Huanuluán; Pilcañeu), *Santa Cruz* (Arroyo Aike; between Swan Lake and Arroyo Aike; Port Desire; Río Chico; Río Coy; Santa Cruz); CHILE: *Magallanes* (Laguna Lazo).

Type.—Adult, skin and skull, British Museum (Natural History) no. 55.12.24.185; collected April, 1934, by Charles Darwin.

Type locality.—Santa Cruz, coast of Santa Cruz, southern Argentina.

Distribution (figs. 70, 75). Patagonian region from western Río Negro and coastal Comodoro Rivadavia (Pico Salamanca), Argentina, south into Magallanes, Chile; altitudinal range, sea level to approximately 1400 meters above.

TABLE 26.—Measurements of *Phyllotis darwini xanthopygus* Waterhouse

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
ARGENTINA							
Huanuluán	126(112–135)27	126(106–135)27	29(28–31)27	—	32.3(31.0–34.0)25	16.5(15.3–17.6)27	5.5(5.1–5.8)27
Pilcañeu	124,128	—,113	28[1],28[1]	28,26	31.4,31.5	16.4,16.4	5.8,5.6
Tecka	130	—	29	28	33.0	17.4	5.8
Río Chico	123,127	119,115	31,31	—	—	—	5.5,5.9
Río Coy	—	—	—	—	31.8,31.9,32.0,32.1	16.6,16.1,16.5,16.8	5.7,5.8,5.7,5.8[2]
Lago Viedma	131	112	32[1]	25	31.5	—	5.7
Santa Cruz[3]	133	97	27.5	—	28	14.5	4.5
Santa Cruz	—	—	—	—	32.3	—	5.8
CHILE							
Laguna Lazo	136,142	112,125	30,30	25,27	32.6,—	17.3,17.3	5.5,5.4

[1] Measured on dry skin, to longest claw.

[2] 6.0 in a fifth specimen with broken skull and no external measurements.

[3] Type of *xanthopygus* Waterhouse; external measurements from original description; cranial and dental measurements from Gyldenstolpe (1932, p. 144); the molar row length is obviously not comparable to other measurements given here.

Characters.—Upper parts more warmly colored, underparts more heavily overlaid with buff or ochraceous and lateral line less defined than in *rupestris;* slightly paler throughout than *fulvescens*, tail more hairy; size as in neighboring populations of *rupestris* (*vaccarum*); pectoral streak usually present and either well defined or confused with the buffy or ochraceous wash of underparts; well-haired tail bicolor except sometimes at tip, length to head and body combined 97 per cent (79–111 per cent, 37 specimens); auditory bullae moderately inflated, their antero-posterior length, less tubes, subequal to alveolar length of molar row; bullar tubes short; width of mesopterygoid fossa, measured at base of hamular processes, subequal to or less than width of parapterygoid fossa at same plane; posterior border of palate rounded, square or angular and without median spine or process; postero-lateral palatal pits anteriad to or in line with posterior border of palate; supraorbital region elongate, the edges square or pinched upward; fronto-parietal suture narrowly rounded or V-shaped; proximal ends of nasals terminating from slightly in front of to slightly behind fronto-maxillary sutures; alveolar length of molar row, 5.6 (5.1–6.0, 41 specimens), or 16–18 per cent of skull length.

Variation.—The transition from pale *rupestris* in the north to the more saturate *xanthopygus* in the south is gradual and appears to be insensible between populations separated by relatively short distances. Specimens from Río Negro (Pilcañeu and Huanuluán) are somewhat more warmly colored on upper parts and underparts than representatives of *rupestris* from Neuquén (Collon Cura; Chos Malal). A specimen of *xanthopygus* from Tecka, Chubut, agrees with the Pilcañeu series. The specimen from the high pampas and scrub country at the base of the Andes in Santa Cruz, first described by J. A. Allen (1905, supra cit.), are more brightly colored than the preceding. The type specimen from Santa Cruz proper on the coast is, according to Thomas (1919b, p. 200), even more buffy on the underparts. Two adults and four juvenals from Lago Lazo, Magallanes, Chile, are darkest and appear to grade into the extremely dark *fulvescens* farther north in Chile. In general, specimens of *xanthopygus* from the Argentine side of the Andes are notably paler than representatives of *darwini*, *fulvescens* and *xanthopygus* of the same latitudes on the Chilean side.

Taxonomy.—*P. d. xanthopygus* is the weakest subspecies of those recognized here. The name represents the southernmost populations of the same comparatively dark ecotypes which range from southern

Peru (*chilensis* of Pearson) through the Andes of Bolivia, Argentina (*ricardulus* and *vaccarum* of Pearson) and Patagonia (*xanthopygus*) to the Straits of Magellan.

Specimens from Neuquén (Collon Cura; Las Lajas; Quilquihue) identified as *xanthopygus* by Pearson, who, evidently, followed Thomas and Osgood, are here referred to *rupestris*. A specimen at hand from Collon Cura, southern Neuquén, is paler than *xanthopygus* from the south but indistinguishable from two individuals of *rupestris* from Chos Malal, Neuquén, and other localities to the north. Unless evidence indicating the contrary is produced, I prefer to regard the *Phyllotis* from the intermediate and ecologically similar localities, Las Lajas and Quilquihue, as likewise representative of *rupestris* (or *vaccarum* of authors).

Measurements.—See Table 26.

Specimens examined.—57. ARGENTINA.—*Chubut:* Tecka, 1 (CNHM). *Río Negro:* Huanuluán, 30 (CNHM, 1; MCZ, 29); Pilcañeu, 3 (CNHM). *Santa Cruz:* Arroyo Aike, 4 (AMNH); Lago Viedma, 1 (MACN); Río Chico, 6 (AMNH, 2; USNM, 4); Río Coy, 5 (USNM); Santa Cruz, 30 miles south along coast, 1 (AMNH). CHILE.—*Magallanes:* Laguna Lazo, Ultima Esperanza, 6 (CNHM).

Phyllotis darwini caprinus Pearson

Phyllotis wolffsohni, Thomas (not Thomas, 1902), 1913, Ann. Mag. Nat. Hist., (8), **11**: 139—ARGENTINA: *Jujuy* (Maimará). Yepes, 1933, Rev. Chilena Hist. Nat., **37**: 47—ARGENTINA: *Jujuy* (Maimará, 2230 meters, 2500 meters). Yepes, 1935, Anal. Mus. argentino Cienc. Nat., **38**: 334—ARGENTINA: *Jujuy* (Maimará). Yepes, 1935, Rev. Inst. Bacteriol. Buenos Aires, **7**: 223—ARGENTINA: *Jujuy*.

Phyllotis ricardulus, Thomas (part, not Thomas, 1902), 1919, Ann. Mag. Nat. Hist., (9), **3**: 493—ARGENTINA: *Jujuy* (Maimará). Thomas, 1921, Ann. Mag. Nat. Hist., (9), **8**: 611—ARGENTINA: *Jujuy* (Alfarcito). Thomas, 1926, Ann. Mag. Nat. Hist., (9), **18**: 194—part, BOLIVIA: *Potosí* (Yuruma).

Phyllotis caprinus Pearson, 1958, Univ. California Publ. Zool., **56**: 406 (fig., molars), 409 (key characters), 434, 435—ARGENTINA: *Jujuy* (Alfarcito; Humahuaca; Maimará; Tilcara; Sierra de Zenta); BOLIVIA: *Chuquisaca* (Camargo), *Potosí* (Yuruma), *Tarija* (Camataquí, 20 miles SSE).

Type.—Adult female, skin and skull, Museum of Vertebrate Zoology, University of California no. 120210; collected 1 October, 1955, by Oliver P. Pearson.

Type locality.—Tilcara, Jujuy, Argentina; altitude, 2500 meters above sea level.

Distribution (figs. 70, 74, 77).—Andes of south central Bolivia from western Chuquisaca, western Tarija and southeastern Potosí, southward into central Jujuy, Argentina; altitudinal range from approximately 2000 to 4650 meters above sea level.

Characters.—Size intermediate between *wolffsohni* and *rupestris* of Bolivia and northern Argentina; color more nearly as in *wolffsohni;* underparts with more buff or ochraceous than *rupestris;* a well-defined pectoral streak present in majority of specimens examined; tail consistently longer than head and body combined, average 122 per cent (101–139 per cent, 35 specimens), bicolor except at tip, short-haired as in *wolffsohni* to long-haired as in *rupestris;* auditory bullae comparatively little inflated, antero-posterior length, less tubes, 4.8 (4.6–5.4, 37 specimens) and approximately equal to or, usually, shorter than alveolar length of molar row (figs. 83, 84); bullar tubes short to moderately long; mesopterygoid fossa, measured at base of hamular processes, from narrower to as wide as parapterygoid fossa measured at same plane, sides parallel or slightly divergent; posterior border of palate notched or with a well-defined unnotched median process; postero-lateral palatal fossa poorly defined, pit small to moderately large and located on a line with or anteriad to posterior border of palate; interorbital region usually flattened as in *wolffsohni,* the edges nearly always square, the posterior halves slightly or not at all beaded, usually divergent posteriorly and sometimes forming narrow ledges; proximal ends of nasals truncate or pointed and terminating on a line with or slightly fore or aft premaxillary sutures; fronto-parietal sutures arced or forming a right angle at midline; molar rows from slightly divergent to slightly convergent posteriorly; enamel pattern of m^2 from modified sigmoid as in *wolffsohni* to 8-shaped as in *rupestris* (fig. 85, *a–c*); m^3 sigmoid, 8-shaped or with second primary fold forming an enamel island which may coalesce with major fold; m_2 sigmoid to 8-shaped; second primary fold present or absent in moderately worn m_{1-2}.

Variation.—Color of upper parts and sides is fairly uniform throughout; underparts are lightly washed with ochraceous in the Tilcara series, most heavily in specimens from Sierra de Zenta and Maimará; a well-developed pectoral streak is present in all Tilcara specimens examined and present in about one-half the specimens of other localities. Tails in the Camargo series of three specimens are extremely hairy, that of the single Tarija specimen the least hairy while tails in the Camataquí series (21 specimens) show a wide variation but generally are as hairy as those of *P. darwini rupestris.*

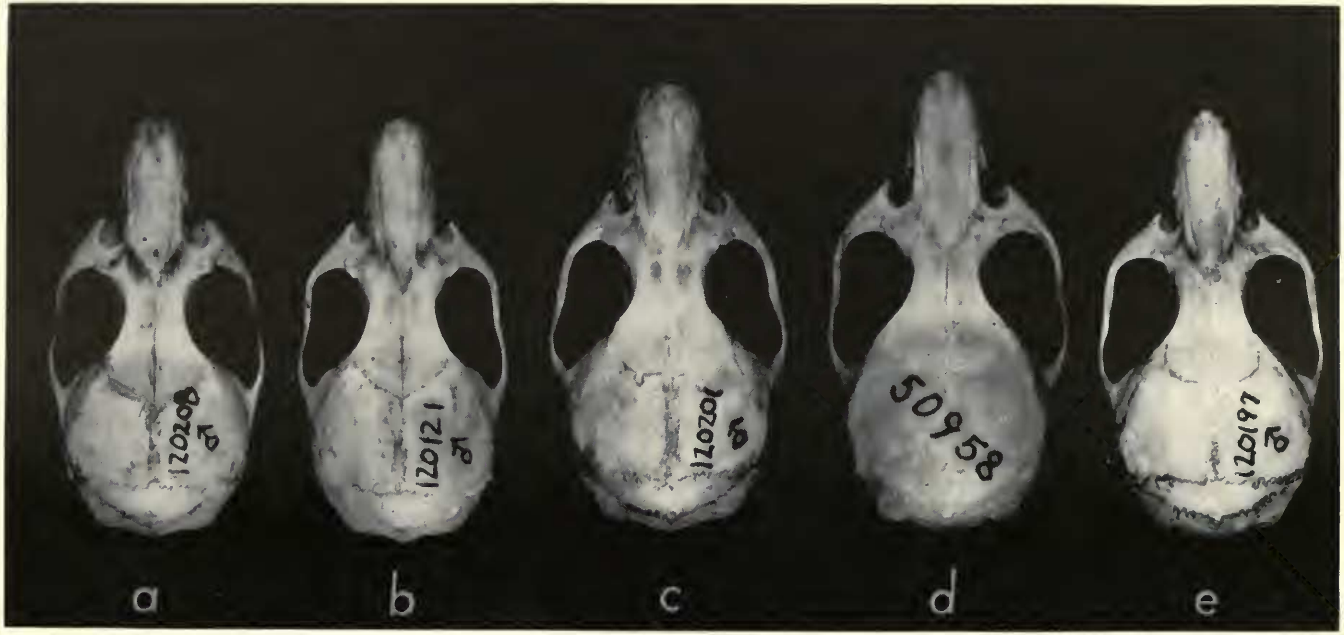
120208
a
120121
b
120201
c
50958
d
120197
e

FIG. 83.—Skulls in dorsal view: *a*, *Phyllotis darwini caprinus* from Tilcara, Jujuy, Argentina; *b*, idem from Camataquí, Tarija, Bolivia; *c*, idem from 5 miles south of Tarija, Tarija, Bolivia; *d*, *Phyllotis darwini wolffsohni* from Taquiña, Cochabamba, Bolivia; *e*, idem from Comarapa, Santa Cruz, Bolivia. (Slightly less than ×2.)

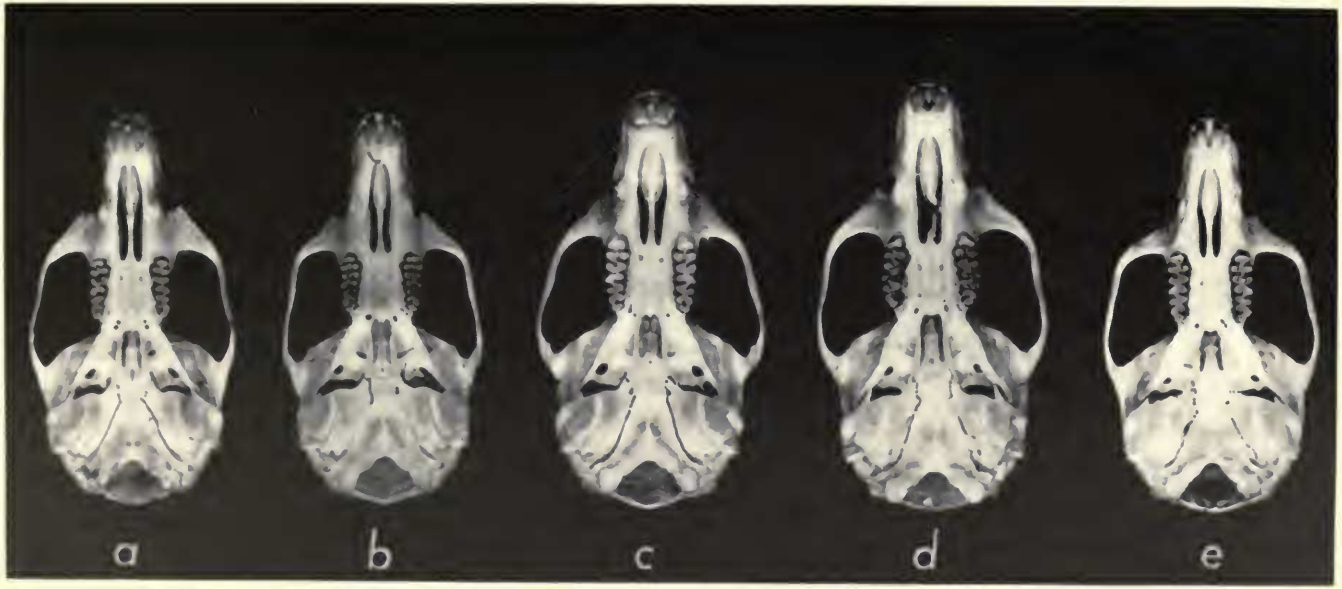

FIG. 84.—Ventral view of skulls shown in figure 83.

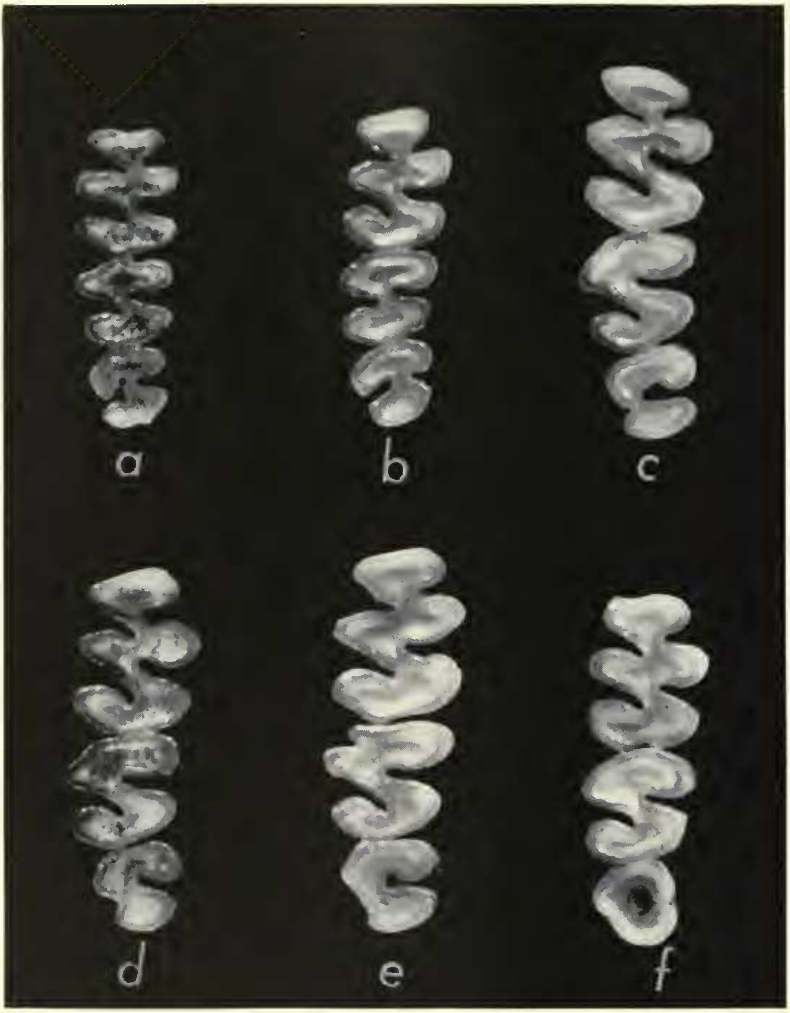

FIG. 85.—Upper molars of *a–c*, *Phyllotis darwini caprinus; d–f, P. d. wolffsohni.*

The fronto-parietal suture is much more sharply V-shaped in the Camataquí than the Tilcara series (fig. 83, *a–c*). In the lone Tarija specimen (MVZ 120201) the suture is broadly rounded as in most *wolffsohni*, the supraorbital region is also more divergent-sided, the edges beaded and with narrow ledges posteriorly as in *wolffsohni*. The enamel pattern of the second and third molars of *caprinus* is the least stable of that in any of the races of *P. darwini*.

Bacula (fig. 7) of the Tilcara series of *caprinus* are like those of *P. darwini rupestris* except that of one subadult which resembles that of adult *wolffsohni*. Bacula of the Bolivian specimens from Camargo, Camataquí and Tarija also agree with those of *wolffsohni*.

Taxonomy.—*Phyllotis caprinus* Pearson was originally described as a full species on the basis of characters which appear to be variable and on geographic considerations which are subject to conflicting interpretations. Pearson (1958, pp. 434, 436) alludes to sympatry between *caprinus* and *darwini* (i.e., *P. darwini rupestris* of this paper). The actual circumstances of "contact" are described (op. cit., pp. 400 401) as follows: "At Tilcara in northern Argentina *caprinus* was captured along brushy hedgerows and stone walls at the edge of the town and *darwini* was taken a few hundred yards east of the town on mountain slopes where tumbled rocks, cardon cactus, *Opuntia*, bromeliads, and *Ephedra* form a more open habitat. Six miles east of Tilcara at Alfarcito where there is a mixture of brushy and open habitat, Budín captured both *darwini* and *caprinus* [see my comments below]. At another location, 25 miles south-southeast of Camataquí, southern Bolivia, the ichu grass of the altiplano meets thornbush, saguaro and other cacti at 11,500 feet. In this mixed habitat I captured many *darwini* but no *caprinus*. Five miles away at 8500 feet among scattered bushes and *Opuntia* I caught large numbers of *caprinus* and no *darwini*." Clearly Pearson's field observations indicate that his *darwini* (i.e., my *P. d. rupestris*) and *caprinus* are completely segregated ecologically and geographically. Budín's nominally sympatric mice may have been taken at a zone of overflow during a population explosion or during a time of temporary mixing of mice driven out of their normally segregated localities by some environmental change such as flood, fire or cultivation. These are speculations based on a possibly incorrect assumption that Budín's Alfarcito representatives of *caprinus* and *darwini* were actually taken in the same trap line or even where contact between the two forms was probable. The Alfarcito specimens were not examined by me but available material indicates that distinction between *caprinus* and *darwini* (i.e., *rupestris*) may be arbitrary.

All specimens of *caprinus* collected by Pearson intergrade morphologically with *darwini*, *wolffsohni* or both. Unfortunately, this fact is obscured in the original description. Of a total of 65 specimens from eight localities examined by Pearson, measurements are given for only 29 or less, all lumped without breakdown to locality. Formal comparisons are made only between 11 topotypes of *caprinus* and 7 specimens of *darwini*, all nominally from Tilcara. The samples of these two populations differ more from each other than from all others known within the geographic area concerned. Tilcara *caprinus* (8 topotypes at hand) averages larger throughout than Tilcara *darwini* (7 specimens at hand), tail less hairy and relatively longer (129 per cent [116–135 per cent] as compared with 110 per cent [98–116 per cent] in *darwini*), pectoral streak consistently present (consistently absent in *darwini*), fronto-parietal suture narrowly arced but not distinctly V-shaped (more widely arced, less sharply V-shaped in *darwini*), supraorbital region flattened, divergent-sided, edges square, beaded or with narrow ledges (less flattened, edges square or pinched upward in *darwini*), zygomatic plate vertical or slanted forward (vertical or slanted back in *darwini*), $m^{\underline{3}}$ with or without an enamel island (island present in all except extremely worn Tilcara *darwini*). In conclusion, only tail pilosity and pectoral streak are constant distinguishing characters, while the others are intergrading.

Camataquí *caprinus* (21 specimens) and *darwini* (8 specimens) agree in color, size (average head and body, 105 versus 104; skull, 28.7 versus 28.3), tail equally hairy but longer relative to head and body (125 per cent versus 114 per cent), pectoral streak present or absent (consistently absent in *darwini*); fronto-parietal suture narrowly to broadly V-shaped in most, arced in others (narrowly to broadly arced in all *darwini*), supraorbital flattened, divergent-sided, edges square (less flattened, edges square to pinched upward), zygomatic plate vertical or inclined backward in both; $m^{\underline{3}}$ with island or more or less 8-shaped in both. No clear distinction can be made here between the two series. It is significant that the larger the number of samples compared, the fewer and vaguer the differences. Considering that the Camataquí populations are not synecetic and perhaps are allopatric, it may be strained to treat each as a peripheral population of *caprinus* and *darwini* respectively, rather than as a pair of well-marked pocket populations of either subspecies.

The relationship of *caprinus* to *wolffsohni* was described in contradictory terms by Pearson. Regarding *caprinus*, Pearson (1958, p. 435) states that "large size, *sharp interorbital edges, frequent absence of the island in* $m^{\underline{3}}$ [italics mine], presence of a second outer entrant notch or angle in $m^{\underline{3}}$ and $m_{\overline{2}}$, and occurrence in bush and thorn scrub habitat occupied by *Graeomys griseoflavus* are all characters [sic] shared at least in part with *Phyllotis wolffsohni*. Geographically they are complementary, and thus suggest status of races."

The same author then concludes that he hesitates "to put into the same species populations in which the skulls can be distinguished so easily (*by shape of* m^3 *and interorbital region* [italics mine]) and in which geographically intermediate populations do not show evidence of intergradation [!]." Inasmuch as Pearson has already described a condition of intergradation between *caprinus* and *wolffsohni* additional evidence of the same is hardly needed here.

A large old male from Tarija (MVZ 120201), collected 25 September, 1955, by Pearson, and geographically referable to *caprinus*, is as much like *wolffsohni* in external and cranial characters (fig. 83,*c*) as anything so identified by Pearson. Its second molars are as in *wolffsohni* and many *caprinus* but m^3, evidently 8-shaped when less worn, is now divided into two laminas (fig. 85,*c*). The Tarija specimen was not mentioned or listed by Pearson with his *caprinus* or any other form of *Phyllotis*.

A few specimens at hand collected by E. Budín in the Maimará and Sierra de Zenta region also show full intergradation between *caprinus*, *wolffsohni* and *rupestris*. A female from Sierra de Zenta (CNHM 85849) taken 28 April, 1947, has the cranial characters of *rupestris*, molars of *wolffsohni*, color characteristics of old pelage "cinnamon phase" *rupestris* and tail as in *rupestris* or many *caprinus*. A male (CNHM 41287) from the same locality, collected 27 July, 1947, is in unworn buffy pelage as in average *caprinus* or Bolivian *rupestris*, its interorbital region is as in *caprinus* and the frontoparietal suture and m^3 as in *rupestris*. A female from Maimará (CNHM 85847) agrees with the preceding cranially and dentally but is intermediate in color between it and the "cinnamon phase" specimen from the Sierra de Zenta.

Individuals of *caprinus* with pectoral streaks and thinly haired tails may be indistinguishable externally from *Phyllotis osilae*. The interorbital region of *osilae*, however, is narrower, the sides pinched, postero-lateral pits generally located on the posterior border of the palate, first primary fold of second and third molars obsolete or absent in the adult and m^3 usually 8-shaped or with *pf* 2 reduced to a large island. In some instances, however, separation from *Phyllotis osilae* can be made only on the basis of subtle (or dubious?) differences in the structure of the glans penis or baculum alone.

Remarks.—*Phyllotis darwini caprinus* is the morphological and geographic bridge between *wolffsohni* and *rupestris*. Its greater resemblance to the first may be the result of a similar response to a similar habitat or may be merely the expression of the same genetic

TABLE 27.—Measurements of *Phyllotis darwini caprinus* Pearson

Locality	Head and body	Tail	Hind foot	Ear	Weight	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
BOLIVIA								
Camargo	98,109,122	128,—,146	26,26,26	23,24,24	34,39,47	28.6,29.7,30.7	15.0,15.4,15.5	5.0,5.2,5.5
Camataquí	105(91–118)21	130(113–146)21	25(24–27)21	24(23–25)21	33(28–56)21	28.7(27.2–31.4)21	14.8(13.9–16.2)21	5.1(4.9–5.3)21
Yuruma	102	130	27	24	—	29.0	15.1	5.2
Tarija	126	132	29	26	—	31.7	16.5	6.3[1]
ARGENTINA								
Zenta	117,109,105	125,113,111	26,28,28	—	—	29.2,31.7,32.3	15.1,16.0,15.5	5.2,5.5,5.6
Maimará	110	128	26	22	—	29.2	—	5.4
Tilcara	113(98–123)8	130(116–135)8	27(27–28)8	25(24–26)8	—	30.3(29.3–32.2)8	15.3(14.6–16.3)8	5.4(4.9–5.6)8
Tilcara[2]	119	133	27	26	—	30.6	15.6	5.4

[1] Means and extremes of length of molar row given by Pearson (1958, Appendix I, p. 464) for 29 specimens of *caprinus* are 5.17 (4.7–5.5). Evidently Pearson overlooked his Tarija specimen (MVZ 120201).

[2] Type of *caprinus* Pearson; measurements from the original description.

constitution. The above synonymy shows that Thomas considered specimens later called *caprinus* by Pearson as indeed inseparable from *wolffsohni*. *P. d. rupestris* occupies a different kind of habitat (cf. Pearson, 1958, pp. 400, 435). Whether near or far from the area occupied by *caprinus* its populations do not appear to be correspondingly more or less like *caprinus*. The lability toward convergence resides with *caprinus*.

Measurements.—See Table 27.

Specimens examined.—40. ARGENTINA. *Jujuy:* Maimará, 2 (CNHM, 1; MACN, 1); Sierra de Zenta, 3 (CNHM, 2; MACN, 1); Tilcara, 9 (AMNH, 8; MVZ, 1). BOLIVIA. *Chuquisaca:* Camargo, 3 (MVZ). *Potosí:* Yuruma, 1 (MVZ). *Tarija:* Camataquí, 21 (MVZ); Tarija, 1 (MVZ).

Phyllotis darwini wolffsohni Thomas

Phyllotis Wolffsohni Thomas, 1902, Ann. Mag. Nat. Hist., (7), 9: 131.

Phyllotis wolffsohni, Pearson, 1958, Univ. California Publ. Zool., 56: 394, 409, 431, fig. 2 (molars), pl. 10, figs. *c*, *d* (skull)—characters; comparisons; BOLIVIA: *Chuquisaca* (Tomina), *Cochabamba* (Arani; Cochabamba; Cuchicanchi; Parotani; Pocona; Punata; Tapacari; Taquiña; Tiraque; Totora), *Santa Cruz* (Comarapa).

Type.—Female, skin and skull, British Museum (Natural History) no. 2.1.1.59 (1.1.1.59 in original description); collected 23 March, 1901, by Perry O. Simons.

Type locality.—Tapacari, west of Cochabamba, Cochabamba, Bolivia; altitude, 3000 meters above sea level.

Distribution (figs. 70, 74, 77).—Andes of central Bolivia in the departments of Cochabamba, extreme western Santa Cruz and northwestern Chuquisaca; altitudinal range 2200 to 3500 meters above sea level.

Characters.—Larger and darker, more brown, than *P. darwini rupestris*, larger than sympatric *Phyllotis osilae;* upper parts buffy to ochraceous coarsely ticked with dark brown; face paler than upper parts; bright ochraceous lateral line nearly always present; underparts sharply defined pale gray to dark gray heavily washed with ochraceous; a well-defined pectoral spot, streak or patch present in majority of specimens examined; hairs of chin and throat not white to base; tail usually longer than head and body combined, average 103 per cent (93–128: 100), bicolor except at tip, short-haired with little or no pencil; auditory bullae comparatively little inflated and less than alveolar length of molar row (figs. 83,*d*–*e*, 84,*d*–*e*), average length, less tubes, 5.1 (4.7–5.5, 25 specimens); bullar tubes short to moderately elongate; mesopterygoid fossa, measured at base of hamular processes, usually narrower, sometimes as wide as parapterygoid fossa measured at same plane, the sides parallel or slightly divergent; posterior border of palate rounded or with a more or less developed median unnotched process; postero-lateral palatal fossa poorly defined, the pit (or pits) small and located in line with or anteriad to posteriad of posterior border of palate; interorbital region usually broad but width at midfrontal plane less than greatest width of rostrum (fig. 83,*d–e*); supraorbital edges sharp, sometimes pinched upward but usually with posterior halves moderately divergent and frequently beaded or forming narrow ledges; proximal ends of nasals usually truncate and terminating behind in a line with or slightly behind premaxillary sutures; molar rows parallel-sided to slightly divergent posteriorly (fig. 84,*d–e*); crown of moderately worn $m^{\underline{2}}$ with a modified sigmoid pattern (fig. 85,*d–f*); anteroloph of $m^{\underline{2}}$ well developed, the first primary fold distinct in unworn to moderately worn tooth but obsolete or absent in worn tooth; crown pattern of $m^{\underline{3}}$ usually more or less sigmoid with first primary fold weak and obsolete in moderately worn tooth, second primary fold usually open to margin, sometimes forming an enamel island, major fold always anteriad to *pf* 2 and sometimes becoming isolated in worn tooth; $m_{\overline{2}}$ sigmoid with minor fold well defined except in very worn tooth; second primary folds present in unworn to moderately worn $m_{\overline{1}-\overline{2}}$; alveolar length of molar row, 5.9 (5.6–6.3, 33 specimens) or 19 per cent (18–21 per cent) of greatest skull length.

Taxonomy.—Phyllotis wolffsohni Thomas was originally distinguished from other members of the *darwini* group by "the striking difference in the shape of the interorbital region" which was described as "much more expanded with marked divergent supraorbital ridges." In 1913, Thomas (p. 139) identified six specimens from Maimará, Jujuy, Argentina, as *Phyllotis wolffsohni* and observed that they were "closely similar to the typical specimens." Later, Thomas (1919a, p. 116) recorded 22 specimens from Chumbicha, Catamarca, Argentina, as "not distinguishable from *Ph. wolffsohni*" and concluded that "the presence of divergent supraorbital edges in the type of *Ph. wolffsohni* . . . appears to be abnormal, or due to great age, as specimens since received are like *Ph. darwini* in this respect." Evidently Thomas was reaching the decision that specific differences between *wolffsohni* and *darwini* did not exist. However, Pearson (1958, pp. 431–2, 434) recognized *wolffsohni* as a full species and restricted the name to central Bolivian material. The species was diagnosed as "an unusually large, long-tailed *Phyllotis* with sharp interorbital edges, heavy rostrum, large tooth row [and] M^2 and M_2 frequently with two deep outer entrant angles." Pearson referred the Chumbicha series identified as *wolffsohni* by Thomas to *Phyllotis darwini ricardulus* and the Maimará *wolffsohni* of Thomas he combined with his own *Phyllotis caprinus.*

None of the characters adduced by Pearson for specific separation of *wolffsohni* from *darwini* and *caprinus* bear scrutiny. Pearson himself emphasized that *wolffsohni* was completely allopatric to neighboring races of *darwini.* His measurements prove that *wolffsohni* is no larger than such races of *P. darwini* as *posticalis, definitus, xanthopygus* and *magister,* and of some populations of any other race including the smallest, *rupestris.* Pearson's measurements also show that *wolffsohni* compares in size with allopatric populations of *Phyllotis osilae.* Proportional differences in size are non-existent and the diagnostic cranial and dental characters of *wolffsohni* are also present as individual and local variables in other races of *darwini,* particularly *posticalis, magister* and *rupestris.* Finally, *Phyllotis darwini caprinus* of southern Bolivia and northern Argentina shows complete gradation from *wolffsohni* to *rupestris* in all characters, particularly in the shape of the baculum (fig. 7). The penis bone of adult *wolffsohni* resembles that of juvenal *P. darwini rupestris.* That of adult *caprinus* is as in *wolffsohni* or *rupestris.*

Variation.—Specimens from Comarapa, Santa Cruz (2345 meters), on the eastern limits of the range are comparatively dark because of the greater density of their guard hairs; the subterminal band of the cover hairs, however, shows the same range from buffy to ochraceous as in other series, including one from Tapacari, Cochabamba (2800 meters), which appears to be palest. Pectoral streaks are better defined and underparts more heavily washed with buff or ochraceous in darker populations. The tail is thinly haired throughout as in *Phyllotis osilae.* The broad supraorbital region with finely beaded edges is well marked in most specimens. In others (e.g., MVZ 120184, Tapacari; MVZ 120197, Comarapa [fig. 83,*e*]) the area is narrower, the edges square or pinched as in representatives of other races (cf. *magister* or *rupestris* from Tarata, Tacna, Peru, and San Pedro, Antofagasta, Chile). The sigmoid pattern of m^3 is more prevalent in *wolffsohni* than any other race of *P. darwini.* This pattern depends on the presence of a well-defined second primary fold open at the margin and entirely posteriad to the major

Table 28.—Measurements of *Phyllotis darwini wolffsohni* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Weight	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
BOLIVIA								
Cochabamba	127,133	123,143	25,27.5[1]	—	—	—,32.1	—,16.5	6.2,5.9
Cuchicanchi	112	143	28	—	—	—	—	—
Parotani	130	140	28	25	—	—	—	5.8
Pocona	140	130	27	25	—	33.1	16.8	6.0
Punata[2]	110,115,119	114,120,118	27,26,26	24,24,24	49,41,55	29.0,29.7,30.2	16.1,16.2,16.3	5.9,6.0,5.9
Punata[3]	112,132	120,143	28,27	25,26	42,65	29.4,32.4	16.0,17.1	5.9,6.0
Tapacari	122(107–135)6	134(122–158)6	27(26–29)6	24(23–26)6	54(43–70)5	30.4(28.1–32.1)6	15.9(15.2–16.6)6	5.85(5.8–5.9)6
Taquiña	130(123–136)6	135(123–141)6	28(27–30)6	24(23–25)6	—	32.1(31.1–32.7)5	16.8(16.4–17.2)5	6.0(5.9–6.1)6
Tiraque	135,135	140,145	27,27	28,28	—	—	—	6.3,—
Tomina	145,145	135,155	27,30	24,24	—	31.3,33.5	16.1,17.4	6.1,5.9
Comarapa	122(115–130)5	127(121–134)5	28(27–29)5	25(24–26)5	52(50–55)4	30.5(30.1–31.0)5	15.9(15.6–16.4)5	5.7(5.6–5.9)5

[1] Dry.

[2] 8 miles NE, 10,000 feet altitude.

[3] 10 miles NE, 10,500 feet altitude.

fold of the opposite side. In 3 of the 29 specimens of *wolffsohni* immediately available, m^3 lacks the usual sigmoid pattern. In the first (MVZ 120194, Comarapa [fig. 85,*f*]) with well worn molars the second primary fold of m^3 is suppressed and the major fold appears as an enamel island. In the remaining two specimens (USNM 271401, Tomina; CNHM 51918, Taquiña [fig. 85,*e*], with molars less worn, *pf* 2 is isolated or suppressed but the major fold is well developed and open to the margin.

Remarks.—*Phyllotis darwini wolffsohni* is the most strongly marked race. Its distinctive characters are the broad supraorbital region and wide fronto-parietal suture, the divergent-sided and frequently beaded supraorbital edges, greater persistence in adults of the first primary fold and the sigmoid pattern of m^3. The same combination of characters though developed to different degrees are also present in partially sympatric *Phyllotis griseoflavus*. On the other hand, sympatric members of *Phyllotis osilae* show none of these characters and are significantly smaller as well. In some localities (Pomata, Cochabamba) the underparts of sympatric *P. osilae* are also darker. Allopatric *wolffsohni* and *osilae* may be indistinguishable in size and external characters but the cranial and dental differences appear to be universal. The same internal characters, larger size and less hairy tail separate *wolffsohni* from Bolivian representatives of *rupestris*. The single specimen of *rupestris* from the geographically nearest locality, Tin Tin, Cochabamba, however, is indistinguishable externally except for smaller size. Elsewhere, in Peru, Chile and Argentina, are populations of *rupestris* with skulls and bodies as large as those of *wolffsohni*. Certain individuals and even entire series of *rupestris* share with *wolffsohni* the sigmoid pattern of m^2 but sigmoid m^3 may be found only in juvenals of *rupestris* and sporadically in adults of other races except *caprinus* where it is frequently present though never as clearly defined as in most *wolffsohni*. Conversely, m^3 of *wolffsohni* is not always clearly sigmoid and its pattern may be as in *rupestris* (cf. Comarapa MVZ 120194 [fig. 85,*f*]) or, more commonly, as in *caprinus*. In no *rupestris* does the interorbital region become quite as broad and square as in most *wolffsohni* although the supraorbital ridges may be as well developed. The nature of the supraorbital region in phyllotines is described elsewhere (p. 57). *Phyllotis darwini magister*, described by Pearson (1958, p. 431) as the counterpart of *wolffsohni* on the western slope of the Andes, is virtually indistinguishable in size and external characters except for its slightly more hairy tail. The enamel pattern of m^2

in some specimens of *magister* from Río Torata, Moquegua, and Arequipa, Arequipa, is as in *wolffsohni* but m^{3} is not sigmoid in adults. The supraorbital region in some *magister* is broad, divergent-sided and beaded as in most *wolffsohni*, while in some *wolffsohni*, the supraorbital region is as in most *magister*. Pearson (1958, p. 432) mentions a slight average difference in the length of the nasals relative to the premaxillae. This is perceptible but adds no weight to Pearson's assumption that "skull differences are great enough to make subspecific relationship [between *magister* and *wolffsohni*] unlikely." Comparison of *wolffsohni* with *caprinus*, its nearest relative, is made under the preceding subspecies heading.

Measurements.—See Table 28 (p. 342).

Specimens examined.—33. BOLIVIA.—*Cochabamba:* Cochabamba, 2 (CNHM); Cuchicanchi, 1 (AMNH); Parotani, 1 (AMNH); Pocona, 1 (CNHM); Punata, 5 (MVZ); Tapacari, 7 (MVZ); Taquiña, 6 (CNHM, 5; MACN, 1); Tiraque, 2 (CNHM, 1; MACN, 1). *Chuquisaca:* Tomina, 2 (USNM). *Santa Cruz:* Comarapa, 5 (MVZ); Guadalupe, 1 (USNM).

Phyllotis osilae J. A. Allen. (Synonymy under subspecies headings.)

Distribution (figs. 70, 74, 77).—Highlands of southern Peru in the departments of Cusco and Puno above 2700 meters southward through the highlands of Bolivia above 1700 meters and northern Argentina as far as southern Catamarca and possibly northern La Rioja; altitudinal range from approximately 500 to 4400 meters above sea level.

External characters.—Size as in *P. darwini* of the same general region; tail from approximately 80 per cent to 130 per cent of head and body length; ears comparatively small, rarely exceeding 25 millimeters measured from notch, and usually less than 23 per cent of combined head and body length; upper parts of body buffy or ochraceous to dark brown, more or less mixed with blackish; underparts rarely sharply defined usually dark gray with plumbeous basal portions of hairs showing through, a thin, sometimes a heavy, buff to ochraceous wash often present; pectoral streak, patch or midventral line usually present; inner and outer sides of ears thinly haired, dark brown, tail short-haired with weakly developed pencil, sharply bicolor or with terminal one-half inch to two-thirds or more of entire length uniformly brown.

Cranial characters (figs. 87, 88).—Interorbital region narrow, parallel-sided or, usually, concave mesially, the borders square, frequently raised or pinched upward and inward, never beaded or forming ledges;

proximal ends of nasals usually pointed and terminating in line with or, usually, behind, rarely slightly in front of, fronto-premaxillary sutures; posterolateral palatal fossa poorly defined, the pit (or pits) variable in diameter but usually small and located posteriad to, often in line with, infrequently anteriad to, posterior border of palate; posterior border of palate usually rounded, sometimes square, rarely incised and often with an unnotched median process; mesopterygoid fossa broad, width at base of hamular processes subequal to width of parapterygoid fossa measured at same plane, sides parallel or slightly concave medially, sometimes slightly divergent; Eustachian tubes usually elongate.

Dental characters.—As in *Phyllotis darwini* but less variable; m^2 more nearly S- than 8-shaped, first primary fold obsolete or absent in moderately worn tooth; *pf* 1 of m^3 absent; *pf* 2 of m^3 nearly always an enamel island.

Comparisons.—The distinctive characters of *Phyllotis osilae* are included in the comparisons made between members of the *Phyllotis darwini* complex and other species of the genus (p. 256). Differences between *P. osilae* and *P. darwini* are idealized in figure 86. The baculum is described and compared in another section (p. 58).

No single character will distinguish *Phyllotis osilae* from other species of the *P. darwini* complex. The shape of the fully developed baculum will separate *Phyllotis osilae* from all adult *P. darwini* with which direct comparison must be made but not from *Phyllotis andium*. The baculum of *P. haggardi* has not been studied but the organ is probably like that of *andium* and *osilae*. Unfortunately, material for comparative studies of the external genitalia of phyllotines is woefully inadequate and most, if not all reliance is placed on other characters.

Much of the geographic range of *P. osilae* overlaps that of *P. darwini*. Except for the structure of the male genitalia, the characters which separate *P. osilae* from *P. darwini* in the regions of sympatry are of the same kind and degree which distinguish allopatric populations and subspecies of either *osilae* or *darwini*. This state of affairs was vaguely recognized and incorrectly interpreted by authors until Pearson (1958, p. 422) provided the necessary data and directions for distinguishing sympatric populations of *P. osilae* and *P. darwini*. The characters adduced by Pearson are listed and discussed below. Those which prove to be of value in separating two or more sympatric populations of *osilae* and *darwini* are summarized in Table 30 and shown in detail in Tables 31–48. The comparisons are based on sympatric series of *osilae* and *darwini* from Peru only. Available material from other areas of sympatry in Tarija, Bolivia (*osilae-caprinus*), Cochabamba, Bolivia (*osilae-wolffsohni*), and northern Argentina (*osilae-rupestris*) is insufficient for the form of analysis made in this part of the text. The particular specimens, however, are described or compared under the pertinent subspecies headings.

A. External

1. *Tail length.*—According to Pearson (1958, pp. 423, 424), the tail of *P. osilae* compared with that of *P. darwini* is longer in the northern part of the range and shorter in the southern. Pearson's conclusions are based on average differences between actual tail lengths of selected individuals identified as "adults" from unspecified localities in each of three "regions of sympatry." Actual or absolute tail lengths may be misleading, and average differences are ordinarily not interpreted as specific differences. I have used the ratio of tail to head and body length for comparisons between individuals and populations of the same or different species. Furthermore only individuals of sympatric series of *osilae* and *darwini* are compared in the following tables and only locally constant or non-intergrading differences, not average differences, are regarded as valid. Tables 30–48 show that the tail of *P. osilae* is proportionately longer than that of *darwini* in 4 of the 18 contact points and shorter in 3. The small number of samples involved suggests that this variation in tail length is purely random. Differences in tail length in the remaining series are average and of no value for separating the species.

2. *Tail pilosity* (fig. 86,*f*).—The individual hairs are visibly shorter in all individuals of *osilae* in 12 of the 18 sympatric series, and the pencil is less if at all developed. The shorter-haired tail of *osilae* may be variously described in other parts of the text as less hairy, less pilose, etc.

3. *Ventral color* (fig. 86,*e*).—The color of belly and chest is apparently darker, i.e., with the dark basal portions of the hairs showing through more prominently in *osilae* than in *darwini*. The real difference between the sympatric populations is not in color but in length of individual hairs, those of *osilae* being shorter with the terminal whitish portion reduced. All individuals of 12 of 18 sympatric series are separable on the basis of the apparent color of the underparts.

4. *Pectoral streak* (fig. 86,*d*). A streak, patch, or mere fleck of buff or ochraceous on the midline of the chest is usually present in *osilae* and frequently absent in *darwini*. In some individuals or populations the streak may develop into a prominent midventral band or become confused with the wash or lining of buff or ochraceous extending over the entire ventral surface. Presence or absence of the streak distinguishes all samples of *osilae* and *darwini* in 10 of the 18 sympatric series and helps in sorting most samples of the remaining series.

Pectoral spotting is usually associated with darker underparts (see 3 above) in both *P. osilae* and *P. darwini*. Clark (1938, p. 79) found pectoral spotting to be a simple Mendelian recessive character in the ecologically similar North American white-footed mouse *Haplomylomys eremicus*. This discovery was confirmed by Dice (1939, p. 14) who also noted that buffy pectoral spots occur more frequently on dark than on pale individuals.

The shorter hair of the tail and underparts and the pectoral streak in *osilae* in localities where *darwini* occurs seem to be parts of a genetic complex independent of environment. Where the species are allopatric, shorter-haired populations occur at lower altitudes and darker ones in more humid localities.

5. *Vibrissae and pelage* (fig. 86,*c*). Pearson (1958, p. 423) notes that the vibrissae are "more slender in *osilae*"and the pelage "less lax and less fluffy, more evenly lined with black in *osilae*." I cannot appreciate any noteworthy or consistent difference in the thickness of the vibrissae but the pelage of the underparts is shorter, hence "less lax" in *osilae* than in *darwini*. These characters cannot be accurately measured or tabulated but may be considered as facets of the same genetic complex discussed in 3 and 4 above.

6. *Ear size* (fig. 86,*a*). The ear of *osilae* is smaller than that of *darwini*. Pearson illustrates the difference in size by absolute measurements and expresses it in terms of average differences. As in the case of tail lengths, absolute ear size is meaningless and usually misleading unless related to the overall size of the animal. The ears of *osilae* never become as large as those of large individuals of *darwini*. On the other hand, small *darwini* may have ears as small or smaller than average-sized or large *osilae*. Furthermore, ears are precociously large in young, and attain their maximum size in adults before maximum body size is reached. Thus, ears are disproportionately large in young individuals, and dispropor-

tionately small in old individuals. In the tables both actual and proportional ear measurements are given but only the latter figures are used for comparative purposes. In either case, ear size proves to be a valid character for sorting nearly all sympatric individuals of *osilae* and *darwini.*

7. *Ear color* (fig. 86,*b*).—"Hairs clothing the inside of the ear pinna are frequently somewhat orange in *darwini* but never in *osilae*. . . ." (Pearson, 1958, p. 423.) This character is exceedingly fine and difficult to appreciate but, nevertheless, surprisingly constant in most sympatric series. The inner side of the ears of *osilae* are usually dark brown with or without a buffy or gray, but not orange or ochraceous, ticking or edging.

B. CRANIAL

1. *Nasals.*—"Nasals in *osilae* come to a point posteriorly that almost always extends farther into the frontals than do the edges of the premaxillae." (Pearson, 1958, p. 423.) This is a valid description but not a reliable distinguishing character. It has diagnostic value in only three pairs of sympatric series, each of which is composed of but a few specimens. Pearson also mentions that in *osilae* the rostrum becomes considerably broader in old age and that "*osilae* tends to have a conspicuous swelling on the side of the rostrum at the premaxillary-maxillary suture." This description applies to all other members of the *P. darwini* group.

2. *Posterolateral palatal pits* (fig. 86,*h,l*).—The pits, often set in fossae, are usually small in *osilae* and nearly always situated posteriad to, often in line with, infrequently anteriad to, posterior border of palate. The converse is true in *darwini* but the character is not constant enough one way or another in either species to be used alone for sorting samples of sympatric *darwini* and *osilae.* The character is further complicated by the fact that the pit of one side is sometimes anteriad while that of the other is in line with or posteriad to the posterior plane of the palate (fig. 86,*l*). Again, there may be two or more pits of equal size variously located on each side of the palate. Position, size and number of posterolateral palatal pits are determined by the number, position and diameter of blood vessels serving the affected area. In spite of its variability and complexity, the pit character is absolutely diagnostic in 7 of the 18 pairs of sympatric series.

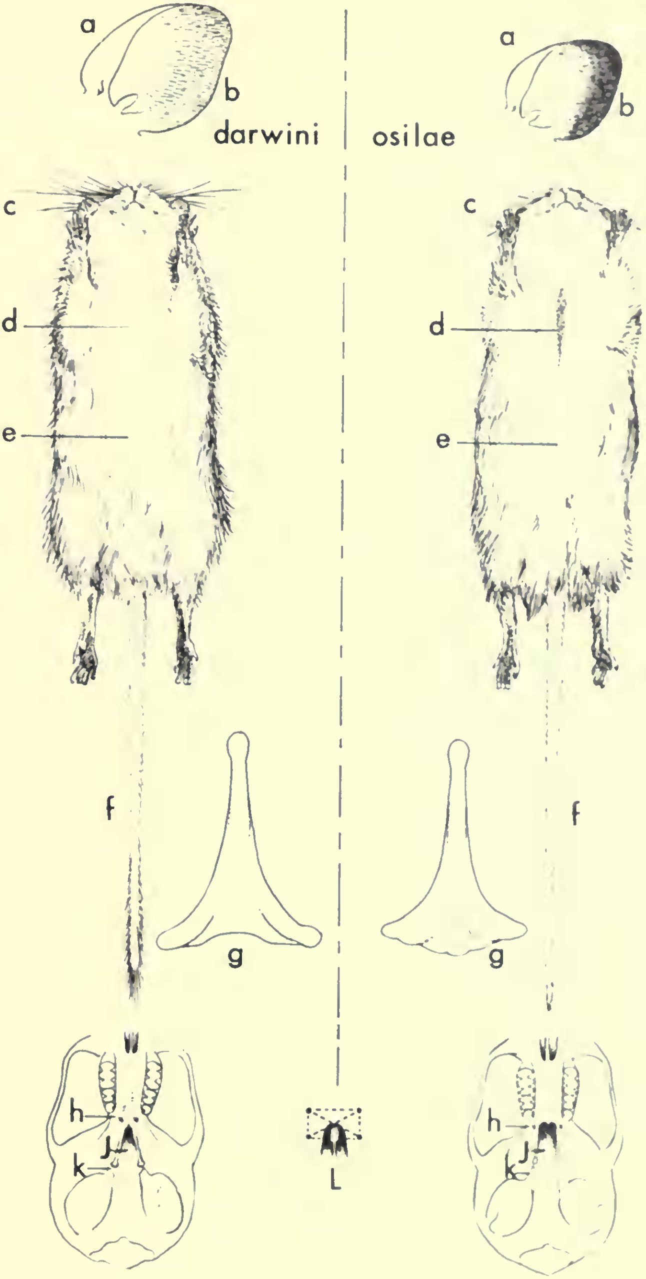
a
b
darwini
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FIG. 86.—Idealized diagnostic characters of *Phyllotis darwini* and *P. osilae*. For explanation of characters see text, pp. 346–348, 350. For their validity and relative constancy in sympatric populations, see Table 30.

3. *Mesopterygoid fossa* (fig. 86,*j*).—The fossa in *osilae* is broad, frequently as wide as or slightly wider than the parapterygoid fossa measured at the anterior base of the pterygoid processes, the sides parallel or slightly concave medially, sometimes divergent. In sympatric *darwini*, the width of the fossa at the anterior base of the pterygoid processes is usually narrower than the parapterygoid fossa measured at the same plane, the sides usually divergent or parallel. The character holds in the majority of the sympatric series examined.

4. *Palatal spine* (fig. 86, not labeled).—Posterior border of palate in *osilae* is usually rounded, sometimes square, rarely cleft in midline and often provided with an unnotched median process. In *darwini*, the posterior border may be rounded or square and often marked by a single unnotched median spine. The character holds in a number of the more poorly represented series.

5. *Palatal width.*—Pearson (1958, p. 423) finds a difference of .28 millimeters between the average width of "38 adult *osilae*" palates and the average of "20 adult *darwini*" palates. The identities or localities of the specimens selected for measurement are not revealed. In any case, the character seems to be more directly related to the size of the individual skulls than to real differences between populations or species.

6. *Bullar tubes* (fig. 86,*k*).—The Eustachian tubes of the auditory bullae are usually elongate and tubular in *osilae*, short, often flattened and strongly ridged in *darwini*. Although its use requires some judgment by the observer, the character holds in nearly every instance where comparisons need be made.

7. *Interorbital region.*—"In *osilae* frequently more pinched than in *darwini* and never with sharp or square edges." Pearson (1958, p. 423). This character is descriptive rather than diagnostic. Pearson notes an average difference of .17 millimeters between the interorbital widths of 38 *osilae* and 47 *darwini*.

C. DENTAL

1. *Enamel pattern of* m^2.—There is little difference between sympatric *osilae* and *darwini* in the enamel pattern of moderately worn m^2. In unworn m^2, the first primary fold is usually less developed in *osilae* than in *darwini* but the difference is not significant. In allopatric *darwini*, *pf* 1 of m^2 may be well developed in the new

tooth and persistent in the worn but it is always weakly developed or obsolete in *osilae*.

Convergence in the enamel pattern of the molars appears to be the rule among closely related cricetines occupying the same or similar habitats.

D. BACULUM

The base of the baculum is convex to nearly plane in adult *osilae* and concave to nearly plane in *darwini* (figs. 6, 7, 86). The baculum is described in a separate section (p. 58).

Variation. Four geographic races, one nominal, are recognized. *Phyllotis osilae osilae* is the centrally located, most widely dispersed and most variable subspecies. It ranges from southern Peru through the Bolivian Andes into northern Argentina. Northward and eastward across the divide into the upper Amazonian drainage in Puno, Peru, and La Paz, Bolivia, *osilae* grades into extremely dark *phaeus*. Continuing southward in Bolivia and northern Argentina, *osilae* becomes progressively more warmly colored and merges with *tucumanus*. *Phyllotis osilae nogalaris* is known only from the type locality, on the eastern slope of the Andes, in Jujuy, Argentina. Its status is uncertain.

Color appears to be the only trenchant character for distinguishing the subspecies of *P. osilae*. As in *P. darwini*, and most mammals for that matter, the more intensely pigmented forms occur in the more humid regions, the more dilute or pale forms in the drier areas. In the case of *P. osilae*, the color cline is almost certainly continuous. Additional material from intermediate collecting localities may prove that there is no real geographic line of separation between the subspecies now admitted.

Habits and habitat. The two original specimens of *Phyllotis osilae* were collected by H. H. Keays at the same localities as *P. boliviensis*. Keays noted that both species had the same habit of feeding on grass during the day. Pearson (1951, p. 144) reports, however, that "several of our specimens were captured at night."

According to Pearson (1958, p. 399) "the long but narrow range of *osilae* will . . . prove to coincide with the distribution of ichu or ichu-like bunch grass . . . [and, p. 424] *osilae* does not enter the tola heaths nor does it live in the brushy and more arid western slopes of the Andes where ichu does not grow well." The altitudinal range of *P. osilae*, from approximately 500 meters (Chumbicha, Catamarca) to somewhere between 4000 and 5000 meters ("Aconquija 13,100–16,400 ft.," Catamarca, fide Pearson, 1958, p. 427) suggests, however, a much wider variety of habitats. The geographic area occupied by *osilae* in the Andes of northern Argentina incorporates the *prepuñena* and *puneña* phytogeographic provinces defined by Cabrera (1953, pp. 130, 145, fig. 12). The first extends from Jujuy to La Rioja between 2300 and 3400 meters above sea level but in some places descends to 800 meters. The province is dominated by bush-steppe and cirriform cacti. The parallel *puneña* province lies between 3400 and 4500 meters above sea level. It is also marked by bush-steppe as well as herbaceous, halophytic and grassy steppes and meadows. The ground in both provinces is largely sand and rock. Altogether it appears that the *prepuneña* and *puneña* provinces combine all the elements said by Pearson to be favored by *P. darwini* rather than *P. osilae*. On the other hand, the next higher district, the *altoandino septentrional*, which lies, according to Cabrera (1953, p. 142), between 4500 and 5500 meters above sea level, is dominated by grasses, including *Festuca* and *Stipa* and should be the preferred habitat of *P. osilae* (fide Pearson). So far, the species has not been recorded from these altitudes.

Reproduction.—Information gathered from notations on skin tags are tabulated below(Table 29) and summarized as follows:

1. Highest proportions of gravid and suckling females appear from April to June.

2. Most males are in breeding condition from December to May.

3. Lowest proportions of gravid and suckling females appear during September and October.

4. Most non-breeding males appear from July to October.

5. Means and extremes of the number of embryos are 4.4 (2–6) 8 specimens.

6. In 5 females for which data are available, the count of embryos in left and right uterine horns, respectively, is 1–5, 2–3, 3–1, 1–1, 2–3.

7. The rough correspondence between ostensible breeding cycles in *P. osilae* and *P. darwini* has been noted. Comments (p. 277) on the reproduction of *P. darwini* also apply to the present species.

Remarks.—The difference in the shape of the base of the baculum and, inferentially, the structure of the soft parts of the glans penis, is slight but is all that stands between regarding *osilae* and *darwini* as sympatric subspecies. Many individuals and entire series of

Phyllotis darwini (sensu lato) are absolutely indistinguishable from *osilae* in the combination of their external, cranial and dental characters. Some of these are geographically intermediate. If the structure of the penis were known from more samples and for all races of *darwini* and *osilae*, possibly its value as a diagnostic character would collapse like all the others. This is suggested by the fact that the bacula of juvenals of *P. darwini* and *P. osilae* are practically indistinguishable.

Phyllotis osilae and *P. darwini rupestris* resemble each other most where they are sympatric. The convergence appears to be restricted to the more widely distributed and plastic *rupestris*. *Phyllotis osilae*, on the other hand, does not tend to become *rupestris*-like anywhere throughout its range. In spite of their similarities interbreeding or hybridization evidently does not take place between sympatric populations of *osilae* and *rupestris*.

In sharp contrast to the above, *Phyllotis osilae* resembles certain allopatric populations of *P. darwini posticalis* more closely than it does sympatric populations of the same form. Thus, for example, sympatric series of *osilae* and *posticalis* are distinguishable by a large number of characters (Tables 44–48) while *osilae* from Choro, Bolivia, is indistinguishable except in overall size from widely separated *P. darwini posticalis* of Palmira, Peru (Table 49). The bacula of the Palmira series, however, are of the *P. darwini* type. Those of the Choro *osilae* are unknown.

The morphology of sympatric series of *P. osilae*, *P. darwini rupestris* and *P. d. posticalis* suggests that all are offshoots from an ancestral *posticalis* stock. Ostensibly, *rupestris* and *posticalis* have always maintained contact at various points while *osilae* became geographically and then reproductively isolated. Subsequent contact between *osilae* and *rupestris* was accompanied by convergence on the part of the more widely ranging and labile *rupestris*. Present overlap in the ranges of *osilae* and *posticalis* is also secondary but available material is too imperfect for determination of the relationship between the forms. On the other hand, contact between *phaeus*, an offshoot of *osilae*, and the peripheral Limbani populations of *posticalis* is a meeting of two terminal twigs of the ancestral divergence (fig. 76).

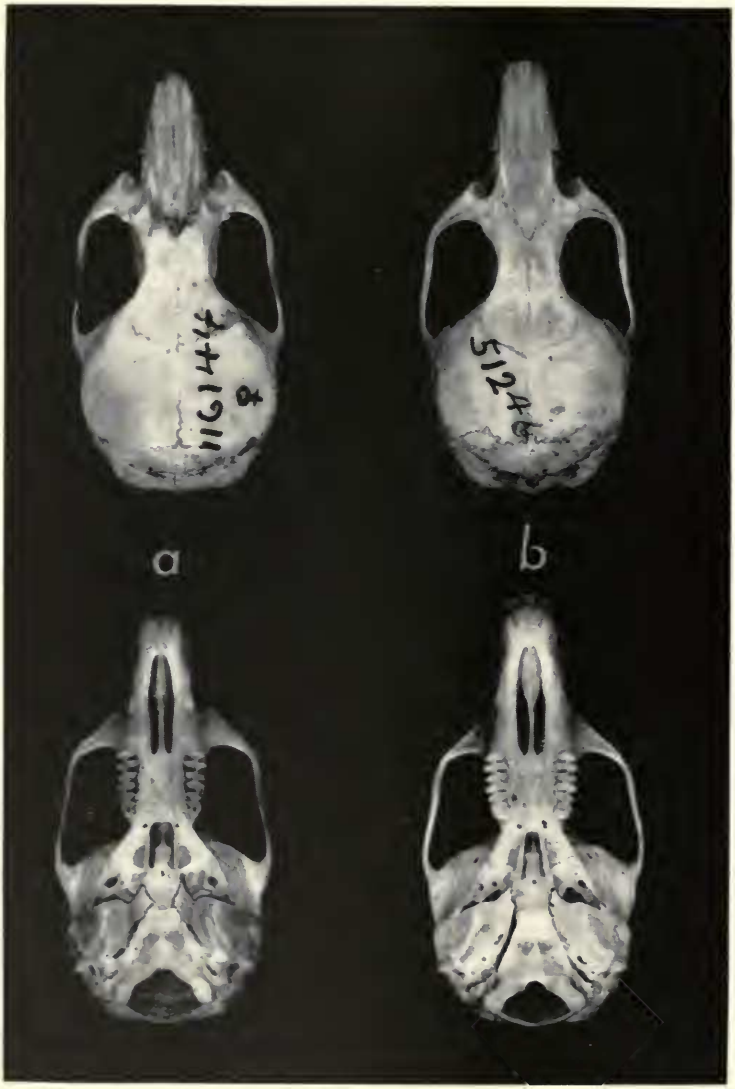


FIG. 87.—Skulls in dorsal and ventral view: *a*, *Phyllotis osilae osilae* from 3 miles west of Asillo, Puno, Peru; *b*, *P. darwini rupestris* from 5 miles south of Asillo. (About × 2.)

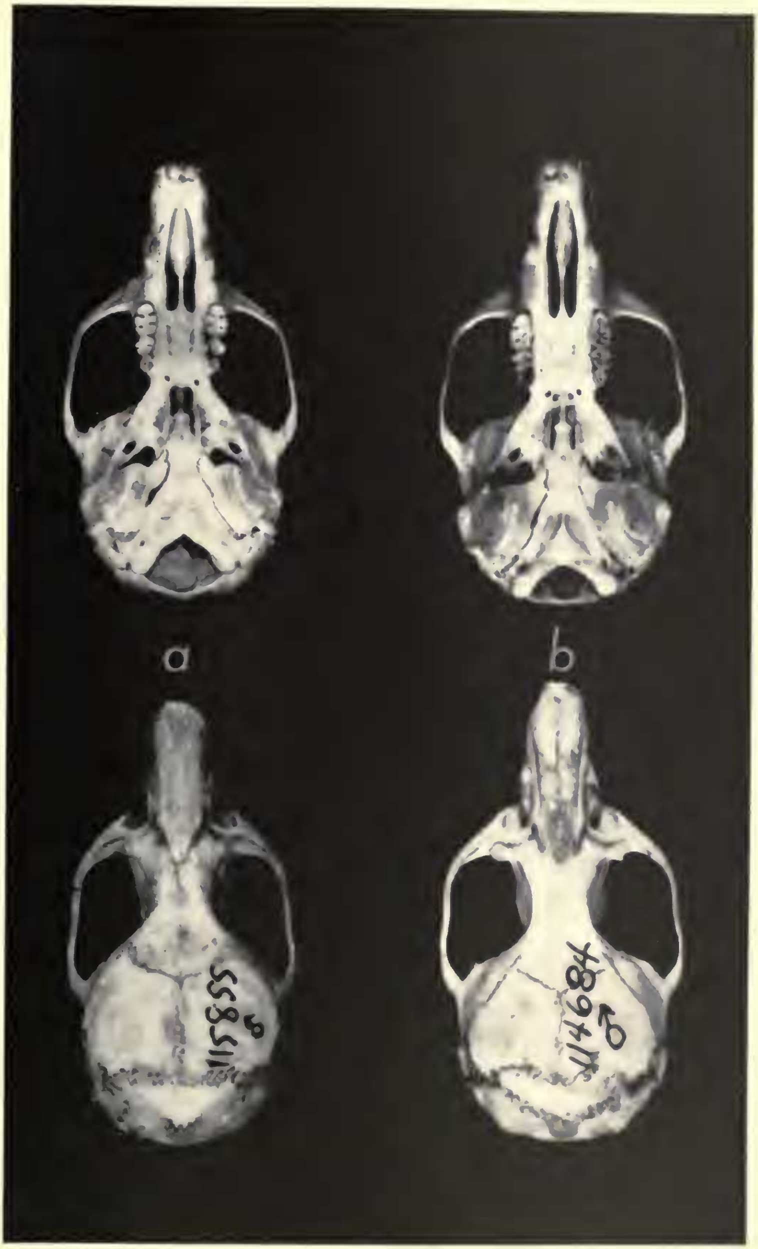


FIG. 88.—Skulls in dorsal and ventral view: *a*, *Phyllotis osilae osilae* from Hacienda Pairumani, Puno; *b*, *P. darwini rupestris* from same locality. Note "*osilae*" type mesopterygoid fossa, bullar tubes and position of postero-lateral palatal pits in *P. darwini*, and "*darwini*" positions of pits in *P. osilae*. (About × 2.)

TABLE 29.—Reproduction in *Phyllotis osilae*

Data from skin tags of specimens collected by O. P. and A. K. Pearson, C. B. and M. Koford and E. Heller. See summary, p. 352.

Month	Locality[1]	♀♀[2]	♂♂[3]
January	Juli, Puno	0,0	10
	Pomata, Puno		7,8,8,9,9.5,10
February	Pairumani, Puno		11,11
	Puno, Puno	0	12
	Vilque, Puno	5	10
April	Ilave, Puno	J,0,0,5,6,L,L,L	J4,J5,J5,J7,9,10,12,13
May	Calacala, Puno	J2,J4,J5,L	J5,10,10,12
	Macchu Picchu, Cusco	4	
June	Arapa, Puno	0	2,3,4
	Calacala, Puno		4,7
	Macchu Picchu, Cusco	4	
	Umayo, Puno	JL	J4,4
August	Limbani, Puno		2,3
September	Punata, Puno	0,0	4,6
	S. Rosa Ayaviri, Puno		6,9
	Tiraque, Cochabamba[4]	0,0,0,0	4,4,4
October	Asillo, Puno	0	
	Limbani, Puno	0,0	6
	León, Jujuy[5]	0	4,5,5
November	Asillo, Puno		7
December	Puno, Puno	0	11

[1] All localities in southern Peru unless otherwise indicated.

[2] Each number (0–6) represents the number of embryos in each female. J=virgin or young; L=lactating.

[3] Each number (4–12) represents length of testes in millimeters in each male; J=juvenal.

[4] Bolivia. [5] Argentina.

Footnotes and explanation of symbols in Table 30

[1] Sympatric series from 13,000 feet.

[2] The 8 specimens of the type series of *P. osilae phaeus* from 11,000 feet and 4 *P. osilae phaeus* from 11,500 feet, compared with 16 *P. darwini posticalis* from 15,000 feet which are not strictly sympatric.

[3] Allopatric *osilae* and *posticalis* alike in all characters compared, with possible exception of baculum.

X=Trait valid for distinguishing all samples of each pair of sympatric series.

o=*Phyllotis osilae osilae*. ph=*Phyllotis osilae phaeus*.

r=*Phyllotis darwini rupestris*. p=*Phyllotis darwini posticalis*.

?=Data unavailable or unknown. R=Reverse relationship of traits.

Blank space=Character not valid for given locality.

TABLE 30. – Comparisons of sympatric series of *Phyllotis osilae* and *P. darwini* in southern Peru

(See opposite page for explanation of symbols, and Tables 31–49 for individual variation in each locality.)

	Subspecies specimens	Ear color	Tail pilosity	Ventral color	Ear:head and body	Bullar tubes	Pectoral streak	Fossa width	Palatal spine	Palatal pits	Tail:head and body	Nasal length	Baculum	Total valid characters
Arapa	o–4 r–1	X	X	X	X	X	X	X	X	X		X	?	10+1?
Puno	o–1 r–2	X	X	X	X	X		X	X	X			X	9
Huacullani	o–3 r–4	X	X	X		X	X	X			X	X	?	8+1?
Occomani	o–2 r–2	X	X	X	X		X		X	X	X		?	8+1?
Puno	o–3 r–3	X	X	X	X	X		X	X				X	8
Juli	o–3 r–5	X	X			X	X	X	X	X			X	8
Asillo	o–3 r–6	X	X	X	X		X	X			X		X	8
Umayo	o–3 r–4	X	X	X	X	X		X					?	6+1?
Pomata	o–7 r–2	X		X		X	X	X					X	6
Chucuito	o–5 r–8	X		X	X	X	X						?	5+1?
Yunguyo	o–12 r–3	X			X		X		X				?	4+1?
Pairumani	o–4 r–3	?	?	?		X	X	X	X				?	4+4?
Pairumani	o–18 r–3		X	X		X							X	4
Ollantaytambo	o–1 p–1	X	X		X	X			X	X	X		?	7+1?
Huaracondo	o–3 p–1	X	X		X	X		?			R	X	?	5+2?+1R
Urco	o–4 p–4			X	X					X	R		?	3+1?+1R
Limbani[1]	ph–1 p–2	X	X	X	X		X	X	R	X	R		X	8+2R
Limbani[2]	ph–12 p–16		X	X			X	X	X			X	X	7
Choro, Bolivia[3] Palmira, Peru[3]	o–5 p–5												?	0+1?
Incidence of Validity (18=100%)		14+1?	13+1?	13+1?	12	12	11	11+1?	9+1R	7	4+3R	4	8+11?	

EXPLANATION OF SYMBOLS

TABLES 31–49: Comparisons of *Phyllotis osilae* with sympatric *Phyllotis darwini*. For descriptions of traits see pp. 346-350 and fig. 86.

A = American Museum of Natural History catalog number.
C = Chicago Natural History Museum catalog number.
H = Museum of Comparative Zoology catalog number.
M = Museum of Vertebrate Zoology catalog number.
U = U. S. National Museum catalog number.
+ = *osilae* trait.
− = *darwini* trait.
o = trait intermediate or indeterminate.
V = valid trait for distinguishing all samples of each sympatric pair of series.
N = invalid trait.
R = traits consistently reversed.
? = data unavailable or unknown.
Blank space = data unavailable or unknown.
s = subadult.
j = juvenal.
t = type specimen.
e = measured on dry skin.

TABLE 31. Comparison of *Phyllotis osilae osilae* J. A. Allen from Arapa, Puno, Peru, with sympatric *P. darwini rupestris* Gervais

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
M 116683 s	29.4	110	123	112	24	22	+	+	+	+	o o	+	+	+	+	
M 116684 s	29.6	111	121	109	24	23	+	+	+	+	+ +	+	+	+	+	
M 116686	30.3	112	125	111	23	21	+	+	+	+	+ +	+	+	+	+	+
M 116687 j	27.2	103	98	95	22	21	+	+	+	+	+ +	+	+	+	+	
rupestris																
M 116685	28.9	112	112	100 N	27	24 V	— V	— V	— V	— V	— — V	— V	— V	— V	— V	?

Explanation of symbols on page 358.

Table 32.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Asillo, Puno, Peru, with sympatric *P. darwini rupestris* Gervais

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
M 116144	29.1	113	125	111	25	19	+	+	+	+	++	+	+	+	+	
M 116145	30.4	115	136	118	25	18	+	+	+	+	++	+	+	+	+	+
A 16503 t	28.1	102	133	130		+	+	+	o	+	++	+	+	–	+	
rupestris																
C 51244	32.3	135	133	99		–	–	–	–	–	– –	–	–	–	–	
C 51245	31.0	127	111	87		–	–	–	–	–	– –	–	–	–	–	
C 51246	30.2	117	109	93		–	–	–	–	–	– –	–	–	–	+	
C 51247 j	28.0	103	97	94		–	–	–	–	–	++	+	–	–	–	
C 51248	29.4	114	111	97		–	–	–	–	–	– –	–	–	–	–	
M 116130	30.3	118	130	110		–	–	–	–	–	– –	–	–	–	–	–
				V		V	V	V	V(?)	V	N	N	V	N	N	V

Explanation of symbols on page 358.

TABLE 33.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Chucuito, Puno, Peru, with sympatric *P. darwini rupestris* Gervais

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
C 52583	27.6	107	109	102	?	+	+	+	+	+	+ +	+	+	+	+	
C 52585	28.7	115	120	104	?	+	+	+	+	+	∓ ∓	−	+	+	+	
C 52587	29.3	126	118	94	?	+	+	+	+	+	o o	−	+	+	+	
C 52593	30.0	123	124	100	?	+	+	+	+	+	o o + +	+	+	+	+	
C 52594	30.2	124	130	105	?	+	+	+	+	+	o o	+	+	+	+	
rupestris																
C 52584	29.0	114	107	94	?	−	−	−	−	−	− ∓	−	−	−	+	
C 52586	29.8	120	108	90	?	−	−	−	−	−	− −	−	+	−	+	
C 52588	28.2	106	97	91	?	−	−	+	−	−	o + o	−	−	−	−	
C 52589	27.9	104	96	92	?	−	−	−	−	−	− −	−	o	−	+	
C 52590	27.1	103	95	92	?	−	−	−	−	−	− −	−	−	−	−	
C 52591	32.4	139	121	87	?	−	−	−	−	−	o −	−	−	−	−	
C 52592	30.5	125	120	96	?	−	−	−	−	−	o o	−	−	−	−	
C 52595		125	110	88	?	−	−	−	−	−	− −	+	−	−	−	
				N	?	V	V	N	V	V	N	N	N	V	N	?

Explanation of symbols on page 358.

Table 34.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Huacullani, Puno, Peru, with sympatric *P. darwini rupestris* Gervais

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
C 52578	—	114	118	104	23	20	+	+	+	+	o o	+	+		+	
C 52579	28.0	107	111	104	22	20	+	+	+	+	— —	o	o	+	+	
C 52596	29.1	114	116	102	23	20	+	+	+	+	— o	+	+	+	+	
rupestris																
C 52576	30.2	105	106	100	25	24	—	—	—	—	— —	—	—	—	—	
C 52577	28.6	118	115	97	24	21	—	—	—	—	— —	—	—	—	—	
C 52580	29.2	124	115	93	27	22	—	—	—	—	— —	—	—	—	—	
C 52581	32.8	140	114	81	28	20	—	—	—	—	— —	—	o	—	—	
				V		N	V	V	V	V	N	N	N	V	V	?

Explanation of symbols on page 358.

TABLE 35.– Comparison of *Phyllotis osilae osilae* J. A. Allen from Juli, Puno, Peru, with sympatric *P. darwini rupestris* Gervais

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
M 115857	31.4	122	139	114	28	23	+	+	+	+	o o	+	+	+	+	+
M 115858	28.5	105	117	111	21	20	+	+	+	+	+ +	+	+	+	+	
M 115859	29.2	114	124	109	21	18	+	+	+	+	o o	+	+	+	+	
rupestris																
M 115818	29.3	105	122	116	26	25	−	−	−	−	− −	−	−	−	+	
M 115819	27.1	92	102	110	22	24	−	−	−	+	− −	−	−	−	−	−
M 115820	29.7	109	123	113	25	23	−	−	−	−	− −	−	−	−	+	
M 115821 j	25.5	89	85	95	22	25	−	−	−	+	− −	−	−	−	−	
M 115885 j	25.8	87	88	101	20	23	−	−	−	+	− −	−	−	−	−	
				N		N	V	V	V	N	V	V	V	V	N	V

Explanation of symbols on page 358.

TABLE 36.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Occomani, Puno, Peru, with sympatric *P. darwini rupestris* Gervais

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
C 53179	30.8	120	130	108		+	+	+	+	+	o +	+	+	+	+	
C 53181	30.3	123	123	98		+	+	+	+	+	+ +	+	+	+	+	
rupestris																
C 53182	31.7	116	116	100		–	–	–	–	–	– –	–	+	–	–	
C 53183	29.6										– –	–	–	–	–	
				V		V	V	V	V	V	V	V	N	N	N	?

Explanation of symbols on page 358.

Table 37.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Pairumani, Puno, Peru (13,500 ft.), with sympatric *P. darwini rupestris* Gervais

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
H 42850 s	27.8	91	105	115	21	23			+		+ +	–	+	+	+	
H 42891		98	102	104	20	20			+		+ ∓	+	+	+	+	
H 42896	27.6	88	100	113	20	23			+		+ +	–	+	+	+	
H 42897	28.5	90	107	119	21	23			+		+ o	+	+	+	+	
rupestris																
H 39518	28.5	99	105	106	25	25			–		– –	–	–	–	–	
H 39519	30.6	110	108	98	25	23			–		– –	–	–	–	–	
H 42906	29.1	108	115	106	25	23			–		∓ –	–	–	–	–	
				N		N	?	?	V	?	N	N	V	V	V	?

Explanation of symbols on page 358.

TABLE 38.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Pairumani, Puno, Peru (13,000 ft.), with sympatric *P. darwini rupestris* Gervais

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
M 114696	32.0	131	130	99	23	18	+	+	+	+	o ō	+	+	+	+	+
M 114697	30.0	120	128	107	24	20	+	+	−	+	o o	+	+	+	+	
M 114698	31.8	131	128	98	24	18	+	+	+	+	o +	+	+	+	+	
M 114699	29.6	125	124	99	23	18	+	+	+	+	+ o	+	+	+	+	
M 114700	31.1	130	127	98	23	18	+	+	+	+	o −	+	+	+	+	
M 114701	30.1	125	129	103	23	18	+	+	+	+	o −	−	+	+	+	
M 114702 s	27.6	105	110	105	22	21	+	+	+	+	− +	−	+	+	+	+
M 114703	31.5	129	120	93	22	17	+	+	+	+	∓ −	+	+	+	+	+
M 114710 s	28.6	105	120	114	22	21	+	+	+	+	o +	+	+	+	+	
M 114711 j	26.7	90	95	95	20	22	+	+	?	+	+ o	+	+	+	+	
M 114712 j	28.0	106	111	105	22	21	+	+	+	+	∓ −	+	+	+	+	
M 114713 s	28.0	100	109	109	22	22	+	+	+	+	o o	+	+	+	+	

(*continued*)

TABLE 38.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Pairumani, Puno, Peru (13,000 ft.), with sympatric *P. darwini rupestris* Gervais (*continued*)

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
M 114714 s	27.8	115	108	94	22	19	+	+	+	+	+ +	+	+	+	+	
M 114715 j		97	114	117	22	23	+	+	+	+	+ o	+	+	+	+	
M 114716 j	27.5	113	115	102	21	18	+	+	+	+	o o	+	+	+	+	
M 114717	30.1	113	123	109	24	21	+	+	−	+	o ∓	−	+	+	+	
M 115855	31.9	124	118	105	22	18	+	+	+	+	− −	−	+	+	+	+
M 115856	31.0	119	120	101	22	19	−	+	+	+	− −	−	+	+	+	+
rupestris																
M 114684	32.0	118	123	104	27	23	+	−	−	−	+ +	−	+	−	−	−
M 115815	29.0	108	114	105	26	24	−	−	−	−	− −	+	−	−	+	
M 115887	31.1	121	121	100	25	21	−	−	−	−	− −	+	−	−	+	−
				N		N	N	V	N	V	N	N	N	V	N	V

Explanation of symbols on page 358.

TABLE 39.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Pomata, Puno, Peru, with sympatric *P. darwini rupestris* Gervais

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
M 115865	32.0	126	147	117	23	18	+	+	+	+	− −	+	+	+	+	+
M 115866	31.0	121	127	105	21	17	+	+	+	+	o +	+	+	+	+	+
M 115867	29.8	122	135	110	22	18	+	+	+	+	− −	−	+	+	+	+
M 115868	30.9	115	133	116	21	18	+	+	+	+	o o	+	+	+	+	+
M 115869	31.1	127	138	109	22	17	+	+	+	+	+ o	+	+	+	+	+
M 115871	30.6	118	127	108	25	21	+	+	+	+	+ ∓	+	+	+	+	+
M 115872	28.7	112	115	103	23	21	+	+	+	+	− −	−	+	+	+	
rupestris																
M 115870	31.2	131	119	109	26	20	−	+	−	−	− −	−	−	−	+	−
M 115873	28.1	105	115	109	26	25	−	−	−	−	− −	−	−	−	−	
				N		N	V	N	V	V	N	N	V	V	N	V

Explanation of symbols on page 358.

TABLE 40.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Puno, Puno, Peru (5 km. W), with sympatric *P. darwini rupestris* Gervais

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
M 115890	31.3	116	117	100	21	18	+	+	–	+	o o	+	+	+	+	+
rupestris																
M 115825	31.2	118	109	92	26	22	–	–	–	–	– –	–	–	–	+	
M 115888	28.8	109	110	100	23	21	–	–	–	–	– –	–	–	–	+	–
				N		V	V	V	N	V	V	V	V	V	N	?

Explanation of symbols on page 358.

TABLE 41.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Puno (15 km. W), Puno, Peru, with sympatric *P. darwini rupestris* Gervais

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
M 115860	28.8	107	117	109	20	19	+	+	−	+	$\overset{-}{o}$ o	+	+	+	+	
M 115861	30.7	120	104	87	22	18	+	+	−	+	+ −	+	+	+	+	+
M 115862	29.4	114	96	84	22	19	+	+	−	+	+ −	+	+	+	+	
rupestris																
M 115826	28.0	100	100	100	24	24	−	−	−	−	− −	−	−	−	+	
M 115889	30.5	123	114	93	26	21	−	−	−	−	− −	−	−	−	+	
M 115891	32.8	126	123	98	26	21	−	−	−	−	− −	−	−	−	+	−
				N		V	V	V	N	V	N	V	V	V	N	V

Explanation of symbols on page 358.

TABLE 42.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Umayo, Puno, Peru, with sympatric *P. darwini rupestris* Gervais

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
M 116692 j	27.4	99	108	109	22	22	+	+	+	+	+ –	–	+	+	+	
M 116693	32.5	108	112	104	22	20	+	+	+	+	+ +	–	+	+	+	
M 116697 j	27.9	106	113	107	23	22	+	+	+	+	o o	–	+	+	+	
rupestris																
M 116691	30.4	114	112	98	26	23	–	–	+	–	– –	–	–	–	+	
M 116694	28.3	105	103	98	24	23	–	–	+	–	o –	–	–	–	–	
M 116695	28.4	103	109	106	24	23	–	–	–	–	– –	–	–	–	–	
M 116696	31.0	118	112	96	27	23	–	–	+	–	– –	–	–	–	–	
				N		V	V	V	N	V	N	N	V	V	N	?

Explanation of symbols on page 358.

TABLE 43.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Yunguyo, Puno, Peru, with sympatric *P. darwini rupestris* Gervais

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
C 51264 j		112	103	92	17	+	+	+	+	+	o o	+	+		+	
C 51265 j	29.1	117	110	94	19	+	+	+	+	–	+ +	+	+	+	+	
C 51267		112	115	103	19	+	+	+	+	+	∓ +	+	+		+	
C 51269	30.8	130	135	103	20	+	+	+	+	+	∓ o	+	+	o	+	
C 51270	30.2	131	120	92	19	+	+	+	+	+	∓ ∓	+	+	+	–	
C 51272 j	27.6	105	109	104	19	+	+	+	+	+	$\overset{o}{+}$ +	+	+	+	+	
C 51273 j	27.4	105	115	109	18	+	+	+	+	+	$\overset{-}{-}$ –	+	+	+	+	
C 51274 j	28.5	109	109	100	19	+	+	+	+	+	$\overset{-}{o}$ +	+	+	+	+	
C 51275 s	28.8	107	118	110	19	+	+	+	+	+	+ –	+	+	o	+	
C 51276	32.3	133	138	103	20	+	+	–	+	+	o ∓	+	+	+	+	
C 51277	31.5	130	130	100	20	+	+	+	+	+	+ o	+	+	–	+	
C 51278		133	112	84	18	+	+	+	+	+	o +	+	+	+	+	
rupestris																
C 51266 j		109	99	91	21	–	–	–	–	–	o –	–	+	?	–	
C 51268	33.2	144	134	93	24	–	–	–	–	–	– –	–	–	?	–	
C 51271 j		106	101	95	21	–	–	–	–	–	– –	–	–	?	+	
				N		V	V	N	V	N	N	V	N	N	N	?

Explanation of symbols on page 358.

Table 44.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Huaracondo, Cusco, Peru, with sympatric *P. darwini posticalis* Thomas

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
C 43389	28.5	125	125	100	21	17	+	+	+	+	− −	−	+	+	+	
U 194713 j	26.6	105	114	109	20	19	+	+	+	+	+ +	+	+	+	+	
U 194714 j	27.8	108	117	108	20	19	+	+	+	+	∓ o	+	+	+	+	
posticalis																
U 194566	34.0	125	142	114	26	21	−	−	+	+	− −	+		−	−	
				R		V	V	V	N	N	N	N	?	V	V	?

Explanation of symbols on page 358.

TABLE 45.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Ollantaytambo, Cusco, Peru, with sympatric *P. darwini posticalis* Thomas

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
U 194722 j	28.0	102	115	112	205	20	+	+	+	+	+ +	+	+	+	+	
posticalis																
U 194577	32.6	130	137	105	24	19	–	–	+	+	– –	–	+	–	+	
				V		V	V	V	N	N	V	V	N	V	N	?

Explanation of symbols on page 358.

TABLE 46.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Hacienda Urco, Cusco, Peru, with sympatric *P. darwini posticalis* Thomas

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
49622	31.5	121	140	116	23	19	+	+	+	+	+ +	−	+	+	+	
49623	30.4	114	133	117	21	18	−	+	+	+	o o	−	+	o	+	
49491	28.8	104	123	118	22	21	+	+	+	+	o +	−	+	+	+	
49494 s	28.7		?	?	20	?	+	+	+	+	+ ∓	−	+	o	+	
posticalis																
49492	28.8	111	130	126	24	22	−	−	+	−	− −	−	+	o	−	
49493	29.8	104	142	136	24.5	24	−	−	−	−	− −	−	+	o	−	
49495	—	104	131	126	22.5	21	−	−	o	−	− −	−	+	−	+	
49497	28.8	103	125	121	23	22	−	−	−	−	− −	+	+	−	+	
				R		N	N	V	N	V	V	N	N	N	N	?

Explanation of symbols on page 358.

TABLE 47.—Comparison of *Phyllotis osilae phaeus* Osgood from Limbani, Puno, Peru (13,000 ft.), with sympatric *P. darwini posticalis* Thomas

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
phaeus																
M 116179	30.6	123	128	104	23	19	+	+	+	+	++	−	+	−	+	
posticalis																
M 116135	29.4	110	130	118	29	26	−	−	−	−	−−	+	−	−	−	
M 116136	30.2	123	140	114	26	21	−	−	−	−	−−	+	−	−	−	−
				R		V	V	V	V	V	V	R	V	N	V	?

Explanation of symbols on page 358.

TABLE 48.—Comparison of *Phyllotis osilae phaeus* Osgood, from Limbani, Puno, Peru (11,000–11,500 ft.), with *P. darwini posticalis* Thomas from Limbani (15,000 ft.)

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
phaeus																
C 52597	29.5	117	128	109			+	+	+	+	+ −	−	+	−	+	
C 52598	31.6	130	140	107			+	+	+	+	+ +	−	+	−	+	
C 52599	29.0	119	118	99			+	+	+	+	+ +	−	+	−	+	
C 52600	30.5	129	125	97			+	+	+	+	+ +	−	+	−	+	
C 53174	31.2	126	135	107			+	+	+	+	o o	−	+	−	+	
C 53175	30.7	114	130	114			+	+	+	+	+ +	−	+	−	+	
C 53176	29.9	128	130	101			+	+	+	+	+ +	−	+	−	+	
C 53177	30.3	123	134	109			+	+	+	+	+ +	−	+	−	+	
M 116175	28.7	108	132	122	25	23	+	+	+	+	+ +	−	+	−	+	
M 116176	29.1	109	138	127	23	21	+	+	+	+	+ +	−	+	−	+	
M 116177	31.5	126	135	107	25	20	+	+	+	+	+ +	−	+	−	+	+
M 116178	28.9	109	124	114	23	21	+	+	+	+	+ +	−	+	−	+	

(continued)

TABLE 18.—Comparison of *Phyllotis osilae phaeus* Osgood, from Limbani, Puno, Peru (11,000–11,500 ft.), with *P. darwini posticalis* Thomas from Limbani (15,000 ft.) (*continued*)

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
posticalis																
M 114675 j	28.0	96	109	114	26	27	–	–	–	–	– o –	+	–	–	–	
M 114676	31.1	119	115	97	29	24	–	–	–	–	– –	+	–	–	–	
M 114677	32.9	127	126	99	30	24	+	–	–	–	– –	+	–	–	–	
M 114678	31.9	123	121	98	29	24	–	–	–	–	– –	+	–	–	–	
M 114679	32.9	127	144	113	31	24	–	–	–	–	– –	+	–	–	–	–
M 114680	31.9	131	117	89	31	24	–	–	–	–	– –	+	–	–	–	–
M 114681 j	27.5	95	116	122	27	28	–	–	–	–	– –	+	–	–	–	
M 114682	30.6	120	118	98	26	22	–	–	–	–	– –	+	–	–	–	
M 114683	32.8	125	132	106	29	23	–	–	–	–	– –	+	–	–	–	–
M 114687		123	136	111	29	24	–	–	–	–	– –	+	–	–	–	
M 114688	29.9	119	123	103	27	23	–	–	–	–	– –	+	–	–	–	
M 114689	29.3	118	127	108	28	24	–	–	–	–	– –	+	–	–	–	
M 114690	29.7	113	106	120	28	25	–	–	–	–	– –	+	–	–	–	
M 114691		120	133	108			–	–	–	–	– –	+	–	–	–	
M 114692	31.3	127	126	99	29	23	–	–	–	–	– –	+	–	–	–	
M 114693	30.4	112	129	115	29	26	–	–	–	–	– –	+	–	–	–	
				N		N		V	V	V	N	V	V	N	V	V

Explanation of symbols on page 358.

TABLE 49.—Comparison of *Phyllotis osilae osilae* J. A. Allen from Choro, Cochabamba, Bolivia, with *P. darwini posticalis* Thomas from Palmira, Apurimac, Peru.

	Skull length	Head and body	Tail	Tail: head and body	Ear	Ear: head and body	Ear color	Tail pilosity	Pectoral streak	Ventral color	Palatal pits (each side)	Palatal spine	Fossa width	Bullar tubes	Nasal length	Baculum
osilae																
C 74868 j	26.5	90	95	105	21	23	+	+	+	+	+ +		+	+	+	
C 74870 s	29.0	105	120	114	20	19	+	+	+	+	o o	–	+	o	+	
C 74871 j	25.7	90	100	111	19	21	+	+	+	+	o o	+	+	–	o	
C 74872 s	28.3	100	120	120	20	20	+	+	–	+	– –	+	+	+	o	
C 74873 s	27.6	95	110	116	20	21	+	+	–	+	+ o	+	–	–	+	
posticalis																
C 75428	31.7	128	140	110	27	21	+	+	+	+	o o	–	–	o	o	
C 75429	33.0	153			28	18	+	+	+	+	– –	–	+	o	+	
C 75430	31.8	129	146	113	26	20	+	+	–	+	– –	–	+	o	o	
C 75431	30.5	115	120	104	25	23	+	+	+	+	+ +	–	+	o	o	
C 75432	30 0	129	121	94	27	21	+	+	–	+	– –	–	+	o	o	
				N		N	N	N	N	N	N	N	N	N	N	?

Explanation of symbols on page 358.

Phyllotis osilae osilae J. A. Allen

Phyllotis osilae J. A. Allen, 1901, Bull. Amer. Mus. Nat. Hist., **14:** 44—PERU: *Puno* (Osila [=Asillo], type locality; Tirapata). Goodwin, 1953, Bull. Amer. Mus. Nat. Hist., **102:** 323—type history; measurements.

Phyllotis osilae subsp., Pearson, 1951, Bull. Mus. Comp. Zool., **106:** 144—PERU: *Puno* (Pairumani).

Phyllotis osilae osilae, Pearson, 1958, Univ. California Publ. Zool., **56:** 422, 426, fig. 6 (penis), pl. 9, figs. *c, d* (skull); pl. 13, fig. *f* (penis bones)—revision; ARGENTINA: *Jujuy;* BOLIVIA: *Cochabamba;* PERU: *Cusco; Puno* [for individual locality records see p. 252].

Phyllotis lutescens Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9:** 131—BOLIVIA: *Cochabamba* (type locality, Choro, 4 km. northeast of Cocapata, Ayopayo Prov., 3500 meters; Choquecamate); *La Paz.* Thomas, 1926, Ann. Mag. Nat. Hist., (9), **17:** 321—BOLIVIA: *Tarija* (Pino [=Piñas]).

[?]*Phyllotis arenarius*, Thomas (part, not Thomas), 1902, Ann. Mag. Nat. Hist., (7), **9:** 224—BOLIVIA: *Potosí* (Lagunillas; El Cabrado).

Phyllotis darwini tucumanus, Thomas (part, not Thomas, 1912), 1918, Ann. Mag. Nat. Hist., (9), **1:** 187—ARGENTINA: *Jujuy* (León).

Phyllotis darwini posticalis, Thomas (part, not Thomas), 1920, Proc. U. S. Nat. Mus., **58:** 230—PERU: *Cusco* (Huaracondo [part]; Macchu Picchu; Occobamba Valley; Ollantaytambo [part]).

Type.—Adult female, American Museum of Natural History no. 16503; collected 17 October, 1900, by H. H. Keays.

Type locality.—Asillo ("Osila"), Puno, Peru; altitude, 3023 meters.

Distribution (figs. 70, 74, 77).—From southern Cusco, Peru, through the Lake Titicaca drainage basin in Puno and western Bolivia, southward through the Andes of La Paz, Cochabamba, eastern Potosí, presumably in western Chuquisaca, Tarija and into the department of Jujuy, northern Argentina; altitudinal range from approximately 1200 to at least 4200 meters above sea level (Hacienda Pairumani, 13,500 feet, O. P. Pearson) and possibly to 4375 (Macchu Picchu, 12,000-14,000 feet, E. Heller).

Characters.—Palest race of *P. osilae;* dorsal surface buffy to tawny finely ticked with dark brown, posterior half of back often more warmly colored than anterior half; lateral line usually ill defined or absent; underparts gray with dark basal portions of hairs showing through; tail longer or shorter than head and body combined, bicolor except at tip.

Variation.—Color of upper parts and sides of *osilae* from Puno, Peru, are virtually identical with those of sympatric *P. darwini rupestris* and vary individually and locally in the same way. Cusco *osilae* resembles darker *P. darwini posticalis* of the same region. Specimens of *osilae* from northern Bolivia (Choro) are darkest and intergrade with extremely dark *P. o. phaeus*. Central and Bolivian *osilae* are more warmly colored, like sympatric *wolffsohni*. Farther south *osilae* grades into the richly colored brown *tucumanus* of northern Argentina. *P. o. osilae* also tends to match its sympatriots in size and bodily proportions. The enamel pattern of the molars of *osilae* is comparatively simple with insignificant individual and local differences. Nevertheless, the tendency for convergence also appears here. The first primary fold of m^2 is obsolete or absent as in sympatric *P. darwini rupestris* but the tooth is more nearly S- than 8-shaped as in sympatric *P. d. wolffsohni* and *P. d. caprinus* to the south.

Other external and local variables are itemized in Tables 30–49 and discussed under the species heading above.

Taxonomy.—The only known character which consistently distinguishes *osilae* from sympatric races of *darwini*, is the shape of the penis bone (and associated soft parts). Any other character which separates sympatric populations of one locality may be a variable in either of the sympatric populations of other localities. Peripheral and allopatric populations of which the genitalia are unknown are assigned to *osilae* or *darwini* primarily on the basis of geography and analogy. Knowledge of the microhabitat of each sample may also aid in the specific determination but the available data are incomplete, generally vague, sometimes subjective, in part contradictory and mostly untested.

Phyllotis lutescens Thomas from Choro, northern Bolivia, described as "a southern representative of the *Ph. Haggardi* of Ecuador" was believed to differ from its nearest geographic ally, *Phyllotis osilae*, by "its shorter tooth-row." The alveolar length of the molar row of the type of *osilae* is 5.1 or 5.2 mm., the crown length about 4.7 mm., not 5.7 mm., as given in the original description. The crown length of the molar row of the type of *lutescens* is given as 4.6 mm., or virtually the same as in *osilae*. On the other hand, available topotypes of *lutescens* are darker throughout than the type and topotypes of *osilae*. Pearson, nevertheless, regards the two named forms as subspecifically inseparable and I accept this solution. Actually, *lutescens* is an intergrade between *osilae* and *phaeus* and could just as well be referred to the one subspecies as to the other.

Measurements.—See Table 50.

TABLE 50.—Measurements of *Phyllotis osilae osilae* J. A. Allen

Locality	Head and body	Tail	Hind foot	Ear	Weight	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
PERU								
Macchu Picchu	115,120	123,125	27,26	21,22	—	28.1,29.9	14.5, —	5.1,5.7
Huaracondo	125	125	25	21	—	28.5	—	5.3
Urco	104,114,121	123,133,140	25,27,25	22,21,23	—	28.8,30.4,31.5	—, —,16.0	5.7,5.4,5.8
Santa Rosa[1]	108,114	113,110	24,26	22,22	—	28.4,29.0	14.8,15.1	5.4,5.3
Asillo[2]	102	133	25[3]	—	—	28.1	14.8	5.2
Asillo	113,115	125,136	27,27	25,25	—	29.1,30.4	14.7,14.7	5.4,5.4
Azangaro	123	124	25	—	—	31.5	16.0	5.0
Calacala[4]	120(107–125)6	127(120–134)6	25.5(24–27)6	24(22–25)6	50(35–55)6	29.6(27.9–30.8)5	15.0(14.3–15.5)5	5.5(5.2–5.8)6
Arapa	110,111,112	123,121,125	27,27,26	24,24,23	39,39,46	29.4,29.6,30.3	15.0,15.2,15.3	5.4,5.0,5.3
Umayo	108	112	25	22	37	32.5	16.3	5.5
Occomani	123,120	121,130	23,25	—	—	30.3,30.8	15.5,16.3	5.3,5.5
Puno	116	117	26	21	52	31.3	15.6	5.3
Puno	107,114,120	117,96,104	24,24,25	20,22,22	37,43,51	28.8,29.4,30.7	14.9,15.5,16.4	5.1,5.1,5.3
Vilque	115,123	100,96	24,24	21,21	40,55	28.7,30.7	15.0,15.8	5.3,5.3
Chucuito	122(115–126)4	122(118–130)4	29(28–29)4	—	—	29.6(29.1–30.4)4	15.2(14.8–15.4)4	5.1(5.0–5.3)4
Juli	105,114,122	117,124,139	25,23,26	21,21,28	35,48,70	28.5,29.2,31.4	14.4,14.5,16.0	5.3,5.2,5.5
Yunguyo[5]	125(112–133)5	128(115–138)5	28(27–29)5	20(18–23)5[3]	—	31.6(30.2–32.2)4	15.9(15.5–16.0)4	5.5(5.3–5.7)4
Pomata[6]	120(112–127)7	132(115–147)7	26(25–27)7	22(21–25)7	54(34–69)7	30.6(28.7–32.0)7	15.4(14.5–15.7)7	5.5(5.1–5.8)7
Pairumani 13,000 ft.[7]	125(113–131)8	126(120–130)8	25(24–26)8	23(22–24)8	58(48–69)8	30.8(29.6–32.0)8	15.8(15.1–16.5)8	5.3(5.1–5.6)8
Pairumani 12,800 ft.	119,124	120,118	26,26	22,22	—	31.0,31.9	15.7,15.7	5.5,5.5

TABLE 50.—Measurements of *Phyllotis osilae osilae* J. A. Allen (*concluded*)

Locality	Head and body	Tail	Hind foot	Ear	Weight	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
BOLIVIA								
Achacachi	136	107	25	21	—	31.0	15.5	5.4
Choro[8]	118	138	25	23	—	29	15.5	4.6
Choro	100,105	120,120	24,26	20,20	—	28.4,29.0	14.7,—	5.3,5.2
Colomi	120	145	27	25	—	31.8	16.5	5.5
Tiraque[9]	107(99–129)7	124(118–133)7	25(25–26)7	21(20–23)7	34(27–46)7	28.7(27.7–30.5)7	14.9(14.7–15.5)7	5.3(5.1–5.4)7
Punata	101	122	26	20	—	28.9	14.4	5.3
Vacas	110	132	24	25	—	—	15.9	5.6
ARGENTINA								
León	102,109,104	129,124,130	27,27,27	21,21,22	—	28.6,29.0,29.7	15.4,15.6,15.2	5.5,5.5,5.6
Yala	114,126,126	123,124,126	27,28,28	—	—	28.8,29.3,30.2	15.8,15.9,15.6	5.6,5.4,5.3

[1] Subadult.

[2] Type of *osilae* J. A. Allen; collector's measurements, total length, 9¼", tail, 5¼", hind foot, 1", are given above in millimeters.

[3] Measurements from dry skin.

[4] Tails of 5 longer, of 1 shorter than combined head and body length; tail: head and body=106 (99–112):100; in four juvenals, tails of 2 longer, 2 shorter; tail: head and body=105 (93–118):100.

[5] Tails of 2 longer, of 2 shorter than combined head and body length and 1 equal; tail: head and body=99 (84–104):100.

[6] Tails of all longer than combined head and body length; tail: head and body=108 (103–117):100.

[7] Tails of 3 longer, of 5 shorter than combined head and body length; tail: head and body=101 (93–109):100. In 8 juvenals and subadults, tails of 7 longer, 1 shorter; tail: head and body=107 (94–118):100.

[8] Type of *lutescens* Thomas; measurements from original description; hind foot without claw; crown length of molar row.

[9] Tails of all longer than combined head and body length; tail: head and body=116 (103–123):100.

Specimens examined.—128. ARGENTINA.—*Jujuy:* León, 1 mile west, 4 (MVZ); mountains west of Yala, 4 (CNHM). BOLIVIA.—*Cochabamba:* Choro, Ayopaya, 5 (CNHM); Colomi, 2 (CNHM, 1; MACN, 1); Punata, 4 (MVZ); Tiraque, 7 (MVZ); Vacas, 3 (CNHM). *La Paz:* Achacachi, Omapuyas, 1 (USNM). *Tarija:* Tarija, 10 miles NW, 1 (MVZ). PERU.—*Cuzco:* Huaracondo, 3 (CNHM); Macchu Picchu, 3 (USNM); Ollantaytambo, 1 (USNM); Tocopoqueyu, Occobamba Valley, 2 (CNHM, 1; USNM, 1); Hacienda Urco, 4 (CNHM). *Puno:* Asillo, 3 (AMNH, the type; MVZ, 2); Arapa, 3 (MVZ); Azangaro, 1 (CNHM); Hacienda Calacala, 10 (MVZ); Chucuito, 5 (CNHM); Juli, 3 (MVZ); Huacullani, 3 (CNHM); Occomani, 2 (CNHM); Hacienda Pairumani, 13,500 feet, 4 (MCZ); Hacienda Pairumani, 13,000 feet, 16 (MVZ); Hacienda Pairumani, 12,800 feet, 2 (MVZ); Pomata, 7 (MVZ); Puno, 1 (CNHM); Puno, 5 km. W, 1 (MVZ); Puno, 15 km. W, 3 (MVZ); Santa Rosa de Ayaviri, 2 (MVZ); Tirapata, 1 (AMNH); Hacienda Umayo, 3 (MVZ); Vilque, 2 (MVZ); Yunguyo, 12 (CNHM).

Phyllotis osilae phaeus Osgood

Phyllotis phaeus Osgood, 1944, Field Mus. Nat. Hist., Zool. Ser., **29**: 193. Sanborn, 1950, Mus. Hist. Nat., "Javier Prado," (A), Zool., no. 5: 5—PERU: *Puno* (Limbani); BOLIVIA: *La Paz* (Pongo; Alaska Mine; Río Aceramarca).

Phyllotis osilae phaeus, Pearson, 1958, Univ. California Publ. Zool., **56**: 427—taxonomic revision; distribution (for individual collecting localities see p. 254).

Type.—Male, skin and skull, Chicago Natural History Museum no. 53177; collected 23 February, 1942, by Colin C. Sanborn.

Type locality.—Limbani, eastern slope of Cordillera Oriental, Puno, Peru; altitude, approximately 3500 meters above sea level. Osgood gives "about 9,000 feet" as the altitude, but this may have been an educated guess. Sanborn collected in the immediate vicinity of and above Limbani, which is at approximately 11,000 feet.

Distribution (figs. 70, 74, 79).—Highlands of southern Peru and northwestern Bolivia in the upper Ríos Inambari and Beni (Ríos Mapiri-Coroico-Boopi) drainage systems; altitudinal range, 3400 to 4300 meters above sea level. The range occupies a narrow belt of heavy rainfall on the Amazonian side of the divide of the Cordillera Real.

Characters.—Darkest member of the *Phyllotis darwini* group; dorsal surface of body heavily lined with dark brown of guardhairs; a blackish mid-dorsal stripe often present; lateral line poorly defined or absent; underparts from pale gray faintly washed with buffy to plumbeous heavily washed with brownish; tail usually longer than head and body combined, never wholly bicolor, pencil and at least terminal one-half inch of underside brown like upper side, sometimes nearly entirely brown.

Variation.—The type series of *phaeus* from Limbani, Puno, consists of 8 specimens including the type (not 9 as stated by Osgood) representing two color phases. Four individuals are extremely dark with plumbeous underparts heavily overlain with brown, tail nearly uniformly brown; the remaining four are less brown, with underparts dark gray thinly washed with brown, tail bicolor except at tip. Four of the specimens were taken from 26 September to 1 October, 1941, the others from 22–23 February, 1942. Both color phases in prime to moderately worn pelage are included in both seasonal crops. A topotype series of 4 specimens collected by C. B. Koford, 11 August to 24 October, 1951 at 3530 meters, also includes both color phases and pelage types. A fifth specimen, taken 24 October, 1951, at 4060 meters, is quite like others from the lower altitudes. All five are practically indistinguishable from the type series except for their longer tails. In the 5 topotypes, the means and extremes of the tail relative to combined head and body length are 115% (104%–127%) and in the type series, 106% (97%–114%). A thin brown median ventral line is present on the tail of all but one of the Limbani specimens and also of some individuals from Pongo, Bolivia and sporadically on the tails of other members of the *P. darwini* group. The palate of the Limbani series is short, its posterior border being on a plane with the posterior borders of m^{3-3} in nearly all samples. The posterolateral palatal pits are posteriad in all five specimens of the topotype series, in six of the type series, and posteriad on the right side and anteriad on the left side in the two remaining specimens. In all, the bullar tubes are short, the proximal ends of the nasals terminating behind the frontomaxillary sutures, the mesopterygoid fossa well opened and the median spinous process usually absent.

Seventy-nine specimens from Pongo in the Cordillera Real, La Paz, Bolivia, collected by G. H. H. Tate, agree with the less saturate color phase of the Limbani series. Their well-defined underparts vary from soiled white to nearly plumbeous; a more or less defined buff or ochraceous pectoral streak is present in about two-thirds of the specimens; in one, the streak is white. Specimens from Río Aceramarca and Alaska Mine agree with those from nearby Pongo.

Four specimens from Tacacoma, La Paz, are paler but each is marked with a well-defined black median dorsal band. Three individuals from Sorata, farther south, are palest, with mid-dorsal surface of body lacking a dark line, and tail sharply bicolor for nearly entire length.

In the La Paz material, the posterolateral palatal pits occupy all possible positions relative to the anterior border of the mesopterygoid fossa. In some, the pits are anteriad, in others posteriad. In still others the pit or pits of one side of the palate may be anteriad, while on the other side they are posteriad to the anterior border of the mesopterygoid fossa. The mesopterygoid fossa may be wide or narrow, the median palatal spine present or absent. The nasals terminate behind the fronto-maxillary suture in all except two individuals where they are on a line with the suture and in one where they terminate in front.

Taxonomy.—The extremely dark *Phyllotis osilae phaeus* is the most differentiated member of the group. The separation of southern Peruvian *phaeus* from pale *P. osilae osilae* is sharp. In northern Bolivia, however, less saturate individuals of *phaeus* from Pongo and nearby localities in La Paz, merge with topotypes of *lutescens* Thomas from Choro, La Paz. Pearson (1958, p. 426) refers the type and Choro series of *lutescens* to typical *osilae* and his classification is followed here. The same material, however, could just as well be treated as extremely pale representatives of *phaeus*. In this case, the name *lutescens* would take precedence over *phaeus*.

Sympatric and quasi-sympatric populations of *P. osilae phaeus* and *P. darwini posticalis* are easily distinguished from each other by a number of mensurable and cranial characters, as well as the marked difference in color. This is in sharp contrast with the *P. osilae osilae*–*P. darwini rupestris* relationship where differences between sympatric populations are, on the average, not as clear as between allopatric populations.

Contact between *posticalis* and *phaeus* is the closing of the ends of a broken chain which began with the former and ended with the latter after separation between intermediates *osilae* and *rupestris* took place (fig. 76).

Measurements.—See Table 51.

Specimens examined.—109. BOLIVIA.—*La Paz:* Alaska Mine, 5 (AMNH); Pongo, 79 (AMNH); Río Aceramarca, 5 (AMNH); Sorata, 3 (AMNH); between Sorata and Tacacoma, 2 (AMNH);

TABLE 51.—Measurements of *Phyllotis osilae phaeus* Osgood

Locality	Head and body	Tail	Hind foot	Weight	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
PERU								
Limbani, 11,500 ft.	113(109–126)4	132(124–135)4	29(28–30)4	40(32–54)4	24(23–25)4	29.5(28.7–31.5)4	15.5(15.2–16.3)4	5.6(5.5–5.8)4
Limbani, 13,000 ft.	128	128	28	47	23	30.6	15.9	5.7
Limbani[1]	123	134	28		19[2]	30.3	15.9	5.6
Limbani[3]	125(114–130)7	129(118–140)7[4]	29(27–31)7		19(18–20)[2]	30.3(29.0–31.6)7	15.9(15.5–16.3)6	5.6(5.5–6.0)7
BOLIVIA								
Tacacoma	122,123,129,134	124,127,140,141	27,26,29,29		—,—,—,—	29.6,30.0,—,31.4	15.3,15.1,—,16.0	5.1,5.1,5.2,5.2
Sorata[5]	104,114,124	110,128,140	25,26,27		—,—,—	27.8,28.9,30.9	14.4,14.7,15.5	5.4,5.4,5.2
Aceramarca	124	—	27		—	30.9	16.1	5.7
Alaska Mine	117(109–121)5	127(121–136)5[6]	27(26–28)5		—	30.7(29.6–32.4)5	15.9(15.5–16.5)5	5.6(5.3–5.8)5
Pongo ♂♂	125(115–137)40	139(123–162)36[7]	28.5(26–30)36		—	31.7(30.3–33.2)30	15.8(14.6–17.0)36	5.6(5.2–6.1)38
Pongo ♀♀	119(110–129)27	134(102–156)27[8]	27.5(25–30)30		—	30.8(29.4–32.2)13	15.6(14.9–16.4)23	5.6(5.3–6.0)28

[1] Type of *phaeus*.

[2] Measurements from dry skin.

[3] Type series.

[4] In 8 specimens, tails of 6 longer, of 2 shorter than combined head and body length. Tail: head and body=(97–114):100.

[5] Subadults.

[6] Tails of all longer than combined head and body length. Tail: head and body=(101–117):100.

[7] In 39 specimens, tails of 35 longer, of 4 shorter than combined head and body length. Tail: head and body=(92–130):100.

[8] In 36 specimens, tails of 33 longer, of 1 shorter than combined head and body length, and 2 equal in length. Tail: head and body=(93–121):100.

Tacacoma, 2 (AMNH). PERU.—*Puno:* Limbani, 8 including the type (CNHM); Limbani, 1 mile S, 4 (MVZ); Limbani, 4 miles SSW, 1 (MVZ).

Phyllotis osilae tucumanus Thomas

Phyllotis darwini tucumanus Thomas, 1912, Ann. Mag. Nat. Hist., (8), **10**: 408.

Phyllotis tucumanus, Thomas, 1919, Ann. Mag. Nat. Hist., (9), **3**: 492—ARGENTINA: *Catamarca* (Otro Cerro). Thomas, 1926, Ann. Mag. Nat. Hist., (9), **17**: 604—ARGENTINA: *Tucumán* (Ñorco, Vipos).

Phyllotis osilae tucumanus, Pearson, 1958, Univ. California Publ. Zool., **56**: 427—revision; ARGENTINA: *Catamarca* (Aconquija; Chumbicha; Las Paras; Otro Cerro; Río Vallecito); *Tucumán* (Cumbre de Mala Mala; La Ciénega; Ñorco; Tafi del Valle; above Tafi del Valle).

Phyllotis sp., Thomas, 1919, Ann. Mag. Nat. Hist., (9), **3**: 116—ARGENTINA: *Catamarca* (Chumbicha [part]).

Type.—Adult female, British Museum (Natural History) no. 4.10.2.6; collected April 10, 1904, by E. Dinelli.

Type locality.—Cumbre de Mala Mala, Sierra de Aconquija, Tucumán, Argentina; altitude, 3300 meters above sea level.

Distribution (figs. 70, 74, 77).—Eastern slope of the Argentine Andes in the provinces of Tucumán and Catamarca; altitudinal range, 500–4000 meters.

Characters.—Warmly colored with more ochraceous than in *osilae;* upper parts of body ochraceous or tawny lined with dark brown and without notable contrast between anterior and posterior parts; lateral line usually indistinct; underparts gray heavily washed with ochraceous; tail comparatively hairy, longer to shorter than combined head and body length; bicolor except at tip.

Variation.—Tails of three specimens from Aconquija are appreciably longer than combined head and body length. In three adults from Tafi del Valle the tail in one is as long as and in two shorter than, head and body combined. Pearson (1958, Appendix I) gives measurements for 38 specimens of *tucumanus* but the relative length of the tails of the various populations cannot be determined from his figures.

Taxonomy.—The systematic position of *tucumanus* as a race of *Phyllotis osilae* rather than of *P. darwini* appears to be correct. Pearson (1958, p. 427) found the "skins of specimens of *tucumanus* difficult to separate from those of *P. darwini* in the same region but skulls separable by . . . the small, lateral posteropalatal pits, long bullar tubes, and narrow rounded interorbital region." How-

Table 52.—Measurements of *Phyllotis osilae tucumanus* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
San Javier	126	131	26[1]	21	30.2	—	5.7
Mala Mala[2]	107	—	24	22	31	15.8	5.2
Tafi del Valle	124	110	30	20	—	—	6.0
Tafi del Valle, above	129,132,140	123,118,140	27,25,30	20,19,24	—	—	—
Aconquija	120	130	25	20	29.0	—	5.7
Vallecito	120,128	115,105	29,29[1]	—	29.7,29.5	16.3,16.2	5.7,5.6

[1] Measured on dry skin.

[2] Type of *tucumanus* Thomas; from original description, external measurements taken on dry skin.

ever, I have examined in the American Museum of Natural History two specimens including a juvenal from Tafi del Valle (2250 meters) that are markedly paler than four warm brown adults from the same named locality but at a higher elevation (3000 meters). The pectoral streak is barely indicated in both, the position of the posterolateral palatal pits anteriad to the posterior border of the palate in the juvenal but not certainly determinable in the damaged skull of the adult. Possibly, these specimens would be better referred to *P. darwini rupestris.*

Measurements.—See Table 52.

Specimens examined.—12. ARGENTINA.—*Catamarca:* Aconquija, 3 (CNHM, 1; MACN, 2); Río Vallecito, Andalgalá, 2 (MACN); Cerro San Javier, 1 (MACN); Tafi del Valle, 2 (AMNH); Tafi del Valle, above, 4 (AMNH).

Phyllotis osilae nogalaris Thomas

Phyllotis nogalaris Thomas, 1921, Ann. Mag. Nat. Hist., (9), 8: 611.

Phyllotis osilae nogalaris, Pearson, 1958, Univ. California Publ. Zool., 56: 427 —ARGENTINA: *Jujuy* (Higuerilla); taxonomy.

Type.—Male, skin and skull, British Museum (Natural History) no. 21.11.1.22; collected 29 May, 1921, by Emilio Budín.

Type locality.—Higuerilla, Jujuy, Argentina; altitude, 2000 meters above sea level.

Distribution (figs. 70, 74, 77).—Known only from the type locality on the eastern slope of the Andes.

Characters.—Known only from the type (and topotype) the original description of which follows:

"A large species of rather dark colour.

"Size large, only exceeded by *Ph. magister.* General colour of the usual grizzled greyish, but darker than usual, about as in dark specimens of *Ph. tucumanus.* Under surface dull whitish, slightly tinged with buffy, which may form a definite patch on the chest. Ears rather smaller than usual, dark brown. Hands and feet white. Tail long, blackish above and at the end, dull white for the proximal half below.

"Skull nearly as large as that of *magister*, its upper outline evenly convex, the middle part of the skull high. Interorbital region very narrow, with well-marked vertically projecting edges, which add to the vertical height of the skull; these, however, have no resemblance to the divergent horizontal beads characteristic of the genus *Graomys*. Zygomatic plate with sharply cut straight front edge. Bullae proportionately rather small.

"Dimensions of the type:—

"Head and body 147 mm.; tail 164; hind foot 30; ear 23.

"Skull; greatest length 35; condylo-incisive length 32.5; zygomatic breadth 19; nasals 14.5 x 5; intertemporal breadth 3.3; breadth of brain-case 15; height of crown from alveolus of m^3 10.6; palatilar length 16; palatal foramina 8.5; upper molar series 5."

In addition Pearson (1958, p. 427) noted that the type had "small bullae, long tubular bullar tubes, lateral [i.e., posterior] posteropalatal pits, and nasals projecting behind premaxillae as in [*Phyllotis*] *osilae tucumanus*."

Taxonomy.—The characterizations and geographic positions detailed above indicate and Pearson (1958, p. 427) affirms that the "two available specimens [of *nogalaris*] are big, old dark members of the *osilae* group" and that their great size "justifies their separation as species."

Remarks.—According to Budín, the collector, this is a "rata de los nogales," or rat of the walnut groves.

Measurements.—See *Characters* above.

Specimens examined.—None.

Phyllotis micropus Waterhouse

Mus micropus Waterhouse, 1837, Proc. Zool. Soc. London, **1837**: 17. Waterhouse, 1839, Zool. Voy. "Beagle," Mamm., p. 61, pl. 20 (animal), pl. 34, fig. 13 (molars)—ARGENTINA: "interior plains of Patagonia, in lat. 50°, near the banks of the Santa Cruz."

Mus (Ab[rothrix]) micropus, Waterhouse, 1837, Proc. Zool. Soc. London, **1837**: 21.

Hesperomys micropus, Burmeister, 1879, Descr. Phys. Rep. Arg., **3**: 217—ARGENTINA: southern Patagonia.

Euneomys micropus, Thomas, 1929, Ann. Mag. Nat. Hist., (10), **4**: 39—ARGENTINA: *Magallanes* (Puerto Prat); *Santa Cruz* (Alta Vista, Lago Argentino).

[*Euneomys* (*Auliscomys*)] *micropus*, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 143—classification.

E[*uneomys*] *micropus*, Thomas, 1919, Ann. Mag. Nat. Hist., (9), **3**: 202—ARGENTINA: *Comodoro Rivadavia* (Koslowsky).

Phyllotis micropus, Allen, 1905, Patagonia Exped., Princeton Univ., **3**, 1, Mamm., p. 60, pl. 12, fig. 13 (skull, molars), pl. 14, fig. 1 (molars)—ARGENTINA: *Santa Cruz* (Swan Lake; Basaltic Canyons; Río Chico Valley); CHILE: Pacific slope. Pearson, 1958, Univ. California Publ.

Zool., **56**: 452—ARGENTINA: *Chubut; Neuquén; Río Negro; Santa Cruz;* CHILE: *Aisén; Cautín; Chiloé; Llanquihué; Magallanes; Malleco.*

Phyllotis (*Auliscomys*) *micropus micropus*, Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 211—revision; ARGENTINA: *Río Negro* (Bariloche, Nahuel Huapi); *Neuquén* (San Martín de los Andes; Sierra de Pilpil); *Chubut* (Valle del Lago Blanco); CHILE: *Magallanes* (Casa Richards, Río Nirehuao; Laguna Lazo; Puerto Natales; Punta Arenas); *Llanquihué* (La Picada; Puella, Lago Todos Santos); *Cautín* (Lonquimai; Río Lolén); Aisén (Río Coihaique); *Malleco* (Sierra Nahuelbuta).

Euneomys micropus alsus Thomas, 1919, Ann. Mag. Nat. Hist., (9), **3**: 302—ARGENTINA (type locality, Maitén, Chubut, 700 meters). Thomas, 1927, op. cit., (9), **19**: 653—ARGENTINA: *Neuquén* (San Martín de los Andes; Sierra de Pilpil); *Chubut* (Epuyen; Barranca, near Tecka). Thomas, 1927, op. cit., (9), **20**: 201—ARGENTINA: *Neuquén* (Quilquihué).

Auliscomys micropus alsus, Yepes, 1935, Anal. Mus. argentino Cienc. Nat., **38**: 335—ARGENTINA: *Neuquén* (Collon Cura).

Phyllotis (*Auliscomys*) *micropus fumipes* Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 214—CHILE: *Chiloé* (type locality, Quellon, Chiloé Island; Río Inio, Chiloé Island).

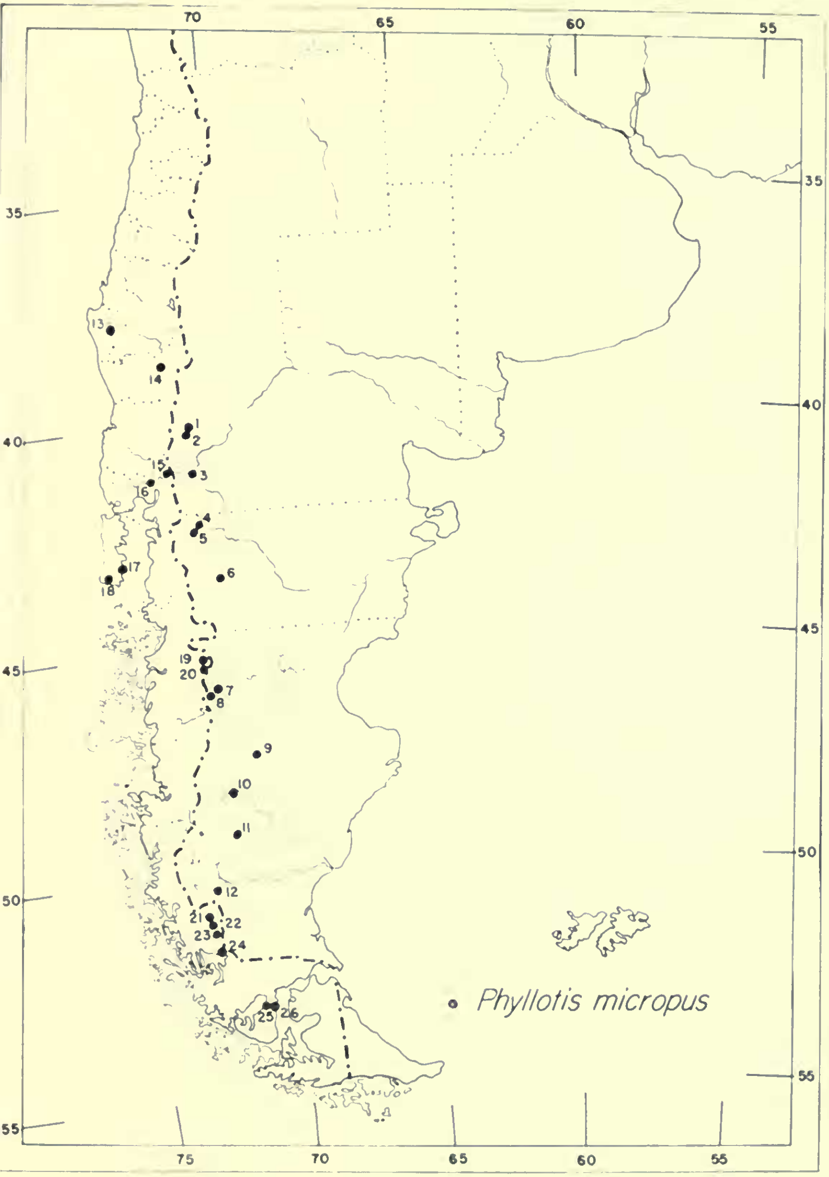
[*Phyllotis* (*Loxodontomys*)] *micropus*, Osgood, 1947, Journ. Mammal., **28**: 172—characterization.

Type.—Adult, British Museum (Natural History) no. 55.12.24.179; collected April 1834, by Charles Darwin.

Type locality.—According to Darwin (*in* Waterhouse, 1839, supra cit.) the type was "caught in the interior plains of Patagonia in lat. 50° near the banks of the Santa Cruz." Darwin relates in Chapter 9 of his "Journal of Researches" (any unabridged edition) that the "Beagle" anchored within the mouth of the Río Santa Cruz in April 13, 1834. On the 18th a party that included Darwin and Captain Fitzroy as commander, started up the river in boats. Toward the end of the month the expedition came within a few miles of the Cordilleras and then turned back. The type of *micropus* was taken at some point along the route, perhaps in the vicinity of the present locality of La Argentina, province of Santa Cruz, southern Argentina.

Distribution (figs. 57, 89).—Southern Chile and southern Argentina from 70° W to the Pacific and from 37° S to the Straits of Magellan; not known from Tierra del Fuego; altitudinal range between sea level and 2000 meters above.

External characters.—Size large, body heavy; tail always shorter than combined head and body length, color of upper side not sharply defined from under side, the terminal portion nearly uniform, pencil rarely developed; hind feet normal, soles lightly scutulated, naked except on heel, plantar tubercles as in *darwini;* ears small, length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● Phyllotis micropus

FIG. 89. Collecting localities of *Phyllotis micropus*. See following page for explanation.

EXPLANATION OF FIGURE 89

Phyllotis micropus: Collecting localities and collectors.

Type localities in **boldface.**

ARGENTINA (1–12)

1. Quilquihué, Neuquén.—E. Budín at 800 meters.
1. San Martín de los Andes, Neuquén.—E. Budín at 1400 meters.
2. Sierra de Pilpil, Neuquén.—South of San Martín; E. Budín at 1200–2000 meters.
2. Collon Curá, Neuquén.
3. Bariloche=San Carlos de Bariloche.
3. San Carlos de Bariloche, Río Negro.—E. Budín at 600 meters; J. L. Peters at 2500 feet.
4. **Maitén, Chubut.**—Type locality of *alsus* Thomas; E. Budín at 700 meters.
5. Epuyen, Chubut.—H. E. Box.
5. Leleque, Chubut (not shown, 35 kilometers southeast of Epuyen).—H. E. Box.
6. Barrancas, near Tecka, Chubut.—E. Budín.
7. Valle del Lago Blanco, Comodoro Rivadavia.—J. Koslowsky.
8. Koslowsky, Comodoro Rivadavia (567 meters).—J. Koslowsky.
9. Swan Lake=Laguna del Cisne, Santa Cruz.—O. A. Peterson.
10. Río Chico Valley, Santa Cruz.—O. A. Peterson.
11. Basaltic Canyons, Santa Cruz.—O. A. Peterson.
12. Alta Vista, Lago Argentino, Santa Cruz.—E. Budín at 600 meters.
12. **La Argentina, Santa Cruz.**—C. Darwin.

CHILE (13–26)

13. Araucaria forest, Nahuelbuta, Malleco.—H. E. Anthony and G. Ottley.
13. Nahuelbuta (Sierra de), Malleco.—C. C. Sanborn.
14. Pinares, Lonquimai, Cautín.—D. S. Bullock at 1600 meters.
14. Río Lolén, Cautín.—C. C. Sanborn at 3600 feet.
14. Araucaria forest, west of Lonquimai, Cautín.
15. Peulla, Lago Todos Santos, Llanquihue.—W. H. Osgood; J. M. Schmidt.
16. La Picada, Volcán Osorio, Llanquihue.—C. C. Sanborn.
17. **Quellon, Chiloé.**—Type locality of *fumipes* Osgood; W. H. Osgood; C. C. Sanborn.
18. Inio (Río), Chiloé.—W. H. Osgood; C. C. Sanborn.
19. Casa Richards, Río Nirehuao.—See Nirehuao (Río).
19. Nirehuao (Río), Aisén.—W. H. Osgood.
20. Coihaique (Río), Aisén.—H. E. Anthony and G. Ottley.
21. Laguna Lazo, Magallanes.—W. H. Osgood; C. C. Sanborn; J. M. Schmidt.
22. Lago Sarmiento, Magallanes.—J. M. Schmidt.
23. Río Verde, Magallanes.—W. H. Osgood; C. C. Sanborn.
24. Puerto Natales, Magallanes.—C. C. Sanborn.
25. Puerto Prat, Magallanes.—E. Budín.
26. Punta Arenas, Magallanes.—W. H. Osgood; C. C. Sanborn; J. M. Schmidt.

from notch one-fourth to one-third less than that of hind foot with claw; postauricular patches reduced or absent, pelage thick, lax, lusterless, the individual hairs finely crinkled; upper parts brown mixed with black and buff, sides slightly paler; underparts not defined from sides, dark gray or plumbeous with an ochraceous suffusion especially on anterior half and mid-line.

Cranial characters (figs. 58–60, 90).—Interorbital region narrow, the sides concave or parallel, borders square or raised, but never ridged or beaded; upper outer angle of fronto-parietal suture with a well-developed burr; zygomata markedly expanded posteriorly, forming a triangular outline when seen from above; greatest zygomatic breadth in adults approximately equal to distance between posterior tips of nasals and anterior border of supraoccipital (usually less in subadults); anterior border of zygomatic plate vertical or sometimes slightly concave, the upper corner rounded or square, never produced as a spinous process; incisive foramina comparatively well opened; posterior border of palatal bridge with a short blunt median process, never square or rounded; bullae moderately inflated, their antero-posterior length, exclusive of tubes, less than, sometimes barely equal to, alveolar length of molar row; outer side of mandible with projecting capsule for encasing base of incisor.

Dental characters (figs. 67, 68, 91).—Incisors extremely thick, opisthodont, ungrooved; molar rows parallel-sided or divergent posteriorly; eruption of third molar retarded as compared with that of *P. darwini;* upper first molar 4-rooted, lower 3-rooted; molars hypsodont, crowns of uppers plane tending to laminate obliquely, those of lowers plane, sometimes slightly terraced, and tending to involution (fig. 17,*c–d*); cusps ovate; paracone and metacone of unworn and moderately worn m^{1-2} inflected forward, metaconid and entoconid of m_{1-2} directed backward, the primary folds forming an angle of about 45° to long axis of teeth; with wear, angle of primary folds becomes progressively wider, approaching a right angle; crown of moderately worn m^2 with modified sigmoid pattern; minor fold of m^2 moderately developed, of m^3 faintly indicated in unworn or slightly worn tooth; procingulum of m^{2-3} well developed, the first primary fold persistent except in extremely worn teeth; postcingulum of m^{2-3} well defined in unworn teeth, the second secondary folds present as enamel islands; vestigial mesoloph sometimes present; minor fold of m_2 moderately developed, of m_3 obsolete; postcingulum of m_{1-2} well developed and persistent except in old teeth; crown pattern of m_3 sigmoid.

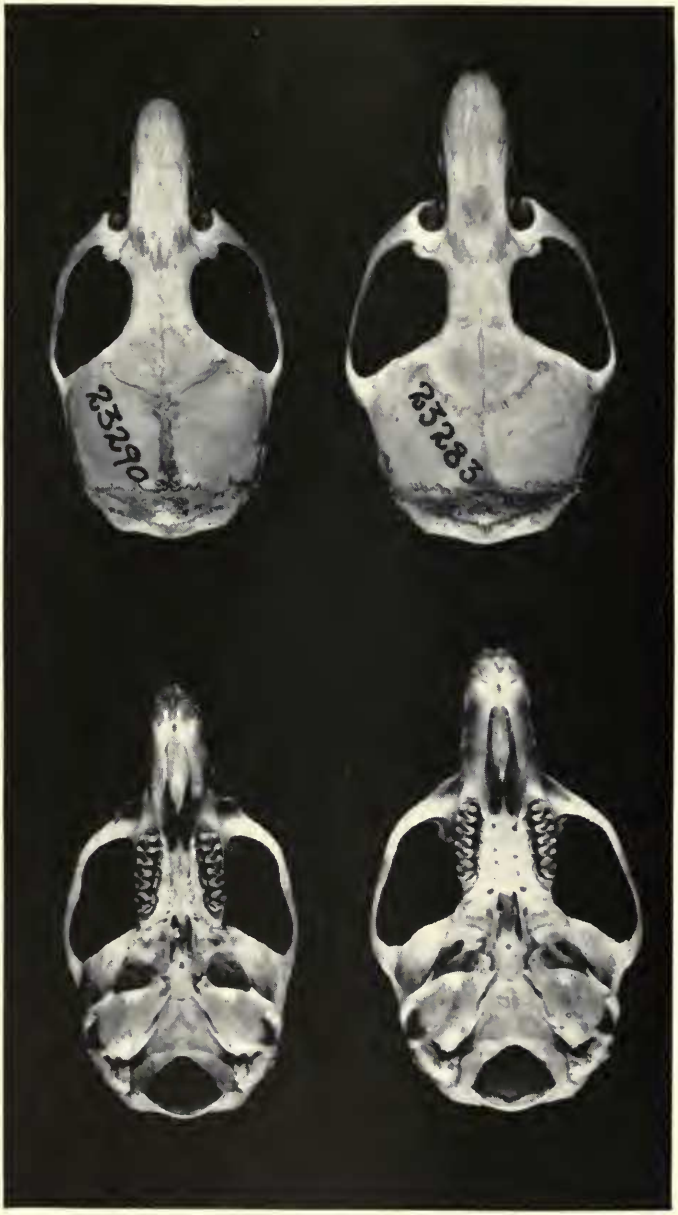
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FIG. 90.—*Phyllotis micropus.* Dorsal and ventral aspects of skulls (× 2).

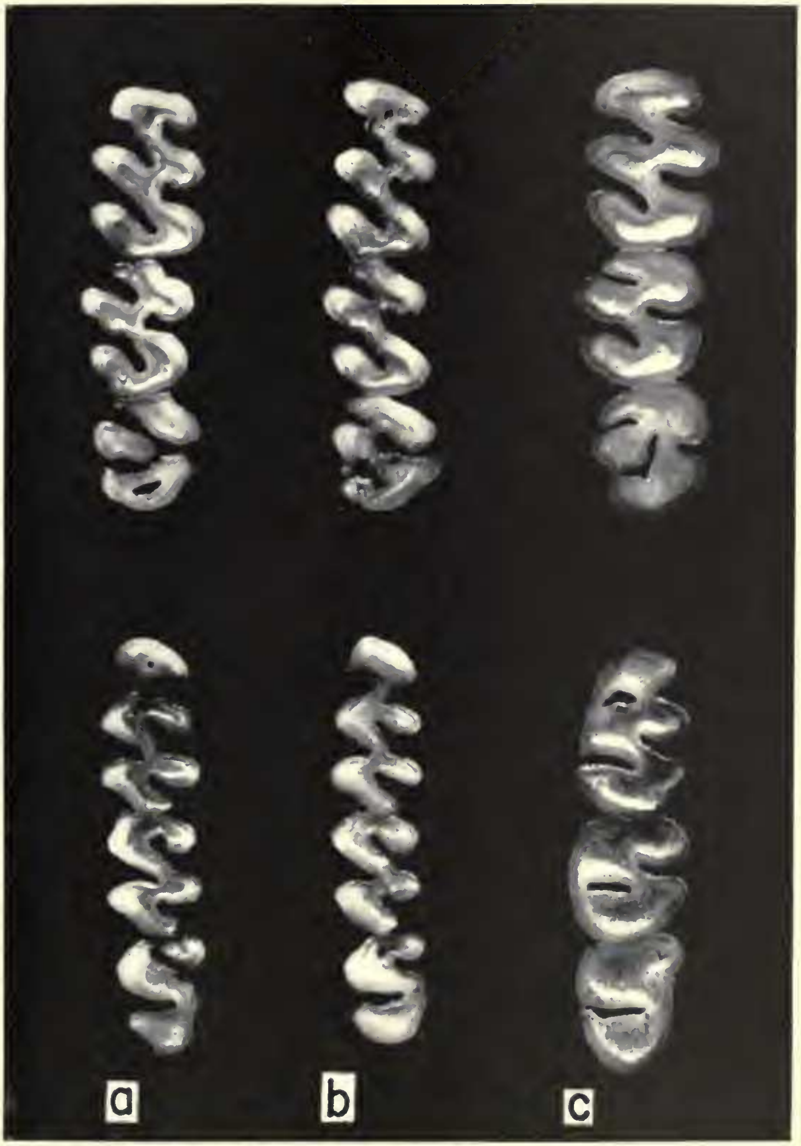

FIG. 91.—*Phyllotis micropus.* Right upper and left lower molars of *a*, juvenal; *b*, subadult; *c*, adult.

Comparisons.—The only comparable species within the geographic range of *Phyllotis micropus* is *P. darwini.* The two resemble each other superficially in form and size, general structure of skull, and gross outline of molars. Important diagnostic characters that permit ready separation of one species from the other are found in the length, color and hairiness of the tail, size of ears relative to body and hind foot, spread and outline of zygomatic arches, thickness of incisors, degree of development of procingula of upper molars and postcingula of lower molars. Thomas (1919b, p. 202) was so far misled by the superficial resemblance between *P. micropus* and *Mus xanthopygus* Waterhouse (a race of *Phyllotis darwini*) that he included the latter along with the former in the genus *Euneomys.*

Phyllotis micropus differs radically in external and cranial characters from the slender, silky furred, white bellied, long hairy-tailed *P. griseoflavus* with divergent-sided supraorbital region. The differences between the two species were used by Osgood (1947, p. 173) to enhance the claims of *micropus* for subgeneric rank. Paradoxically, the greatest resemblance between *micropus* and *griseoflavus* lies in the dental characters (fig. 67) described by Osgood as "unique" in the former. The development of the procingulum and persistence of the first primary fold in the second upper molar is about the same in both species. The forward inflection of the metacone is also similar in both but the paracone, always oblique in unworn to moderately worn molars of *P. micropus,* is not consistently flexed to the same extent in comparable molars of *P. griseoflavus.* Similar oblique positions of cusps and primary folds have been noted in unworn to slightly worn molars in some forms of *Phyllotis darwini,* particularly *P. d. wolffsohni,* in *Phyllotis pictus* and in all but greatly worn molars of *Euneomys chinchilloides* (fig. 123). In *P. pictus* the procingulum of m^2 is as well developed as in *micropus;* in *P. darwini wolffsohni* it is less well developed and in *Euneomys* the procingulum is considerably reduced, and obsolete or absent in the worn tooth. The incisors of *pictus* are orthodont, weakly grooved and more delicate than in *micropus;* in *Euneomys* they are opisthodont and strongly grooved, though quite as robust as in *micropus.* Both *Phyllotis micropus* and *Euneomys chinchilloides* are heavy bodied, lax furred, dark bellied, short tailed, and small eared. The tail of *Euneomys,* however, is shorter (always less than 60 per cent of combined head and body length in adults) and sharply bicolor throughout its length. Cranially, *Phyllotis micropus* and *Euneomys* are widely separated (cf. p. 496).

Variation.—Individual, local and seasonal differences in *P. micropus* are slight. Geographic variation, if it exists, is not appreciable. The geographic area occupied by the species is comparatively small, its climate uniform.

The left upper incisor of a specimen (CNHM 50615) from Punta Arenas was described by Osgood (1943, p. 211) as "distinctly grooved." From this, Osgood inferred that the relationship between *micropus* and the normally grooved-tooth *pictus* was intimate and he included both in his genus *Auliscomys*. This classification was later rejected by Osgood (1947, p. 172). An examination of the incisor in question reveals the "groove" as a traumatic condition.

Habits and habitat.—Mr. O. A. Peterson, who collected *Phyllotis micropus* in Patagonia, records (*in* Allen, 1905, p. 61) that "this is the most common species met with on the 'Rio Chico Cordillera, especially in the heavy grass near water; but was also caught in timber at some distance from water.' " Allen (supra cit.) added that "it appears to have been rare further north in the more open country where Mr. Colburn worked, he securing only four specimens during six weeks of constant trapping."

Judged by the nature of the collecting localities, *Phyllotis micropus* is essentially a forest glade dweller, but maintains itself in high grass and brush on the banks of streams in deforested country as well. The retarded eruption of the third molar in *P. micropus* is generally characteristic of forest dwelling cricetines. In deforested areas, *micropus* and invading representatives of *P. darwini* may be found in the same locality but not necessarily in the same habitat.

Taxonomy.—*Loxodontomys* Osgood, 1947, was proposed as a subgenus of *Phyllotis* to contain only *Mus micropus* Waterhouse. This classification would be justified, as indeed it was, on the scale of values that determines each aggregation of subspecies and their synonyms as a "species group," and each well defined species as a subgenus or genus. The "*Phyllotis* group," as understood by Osgood, and by Thomas as well, is nothing more than the *P. darwini* complex of this paper. *Graomys*, as conceived by the same authorities, is merely *P. griseoflavus*. *Paralomys* is *P. gerbillus*. Rejection of this inflated classification eliminates the need for the name *Loxodontomys* and leaves its species occupying exactly the same phylogenetic position relative to all other species of the genus *Phyllotis*.

Euneomys micropus alsus Thomas was sunk into the synonymy of *Phyllotis micropus* by Osgood. No particular reason was given for this action, but material at hand shows no basis for subdivision

Table 53.—Measurements of *Phyllotis micropus* Waterhouse

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
ARGENTINA							
Santa Cruz[1]	152	97	27	13	—	—	—
Río Chico	130	90	29	—	32.2	—	5.8
Lago Blanco	121,137	92,93	29,28	—,21	31.3,31.5	17.8,17.9	6.0,6.1
Maitén[2]	123	117	27	18	31.3	18.0	5.7
Pilpil	124	96	27	18	—	18.1	6.1
Bariloche	123,127,134	108,103,96	27,28,28	18, ,20	31.4,30.0,32.1	17.2,16.9,18.0	6.3,5.8,5.8
San Martín	136	98	26	19	—	—	5.7
CHILE							
Punta Arenas	144(130-156)19	102(93-115)18	30(28-32)19	—	32.9(30.8-34)18	18.9(17.8-20.3)18	6.0(5.8-6.4)19
Pto. Natales	149	109	31	—	—	19.2	6.0
Río Verde	132,143	98,97	30,30		32.0,33.2	18.4,19.3	5.9,6.1
L. Sarmiento	122,129,136	95,102,94	27,30,27	—,—,—	31.1,31.2,32.1	18.0,17.8,18.5	5.7,5.5,5.8
L. Lazo	137(122-143)8	101(92-107)8	29(28-30)8	—	32.4(31.6-33.2)8	18.7(18.3-19.0)7	5.9(5.6-6.1)8
Coihaique	124,133	101,93	30,29	—,—	31.4,31.2	17.5,16.7	5.5,5.8
Río Nirehuao	138(124-157)20	100(92-108)19	28(27-29)20	—	32.3(30.9-34.2)19	17.9(16.8-19.2)18	6.0(5.6-6.4)19
Chiloé[3]	124	90	29.5	—	29.8	16.8	6.2
Peulla	131,149	121,106	31,32.5	—,—	33.8,—	18.9,—	6.6,6.3
La Picada	131	114	32	20	32.6	18.5	6.5
Río Lolén	114	99	29		31.9	17.6	6.0
Nahuelbuta	132,131,135	107,106,104	31,30,30		—,31.8,—	17.7,17.8,18.1	5.8,5.4,5.8

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[1] Type of *micropus* Waterhouse, from original description.

[2] Type of *alsus* Thomas, from original description.

[3] Type of *fumipes* Osgood.

of the species into races. The distinctive color attributed to *alsus*, as compared with Río Chico, Santa Cruz representatives of *micropus*, is on the same order as that which distinguishes one specimen from another of the same locality.

Phyllotis micropus fumipes Osgood, from Chiloé Island, is based on four specimens "all of them somewhat immature." Their characters are said to be "practically as in *micropus* except that the hands and feet are darker." The four members of the type series are better described as juvenals, the type being the oldest. In these, upper surface of feet is dark because the brown skin is thinly covered with short silvery hairs. Feet of mainland individuals of comparable age are similar. In most adults, however, the feet are more thickly haired, hence less brown in appearance.

Measurements.—See Table 53.

Specimens examined.—103. ARGENTINA. —*Chubut:* Valle del Lago Blanco, 2 (CNHM). *Neuquén:* San Martín de los Andes, 1 (CNHM); Sierra de Pilpil, 1 (CNHM). *Río Negro:* San Carlos de Bariloche, 7 miles east, 3 (CNHM). *Santa Cruz:* Río Chico, Cordillera, 5 (AMNH, 4; CNHM, 1). CHILE. *Aisén:* Coihaique, 10 (AMNH). *Cautín:* Río Lolén, 1 (CNHM); Pinares, Lonquimai, 1 (CNHM); Araucaria forest west of Lonquimai, 1 (AMNH). *Chiloé*; Río Inio, 3 (CNHM); Quellón, type of *fumipes* Osgood (CNHM). *Llanquihue:* La Picada, Volcán Osorio, 1 (CNHM); Puella, Lago Todos Santos, 2 (CNHM); Río Nirehuao, 24 (CNHM). *Magallanes:* Laguna Lazo, 9 (CNHM); Lago Sarmiento, 3 (CNHM); Puerto Natales, 1 (CNHM); Punta Arenas, 21 (CNHM); Río Verde, 7 (CNHM). *Malleco:* Araucaria forest, Nahuelbuta, Malleco, 3 (AMNH); Sierra de Nahuelbuta, 3 (CNHM).

EXPLANATION OF FIGURE 92

Phyllotis pictus: Collecting localities and collectors.
Type localities in **boldface**.

Phyllotis pictus (1–35)

PERU

1. Quilcayhuanca, Ancash. C. Kalinowski at 4000 meters.
2. Catac (Hacienda), Ticapampa, Ancash. C. Kalinowski at 4000 meters.
3. Chipa, Pasco. H. Watkins at 12,400 meters.
4. Carhuamayo, Junín. C. C. Sanborn at 14,500 feet.
5. San Blas, Junín (approximately 4000 meters). J. Kalinowski (father of C. Kalinowski), at "18,000 feet," an impossible altitude for the region.
6. **Junín, Junín.** M. P. Anderson at 14,000–14,500 feet.

Explanation of Figure 92 (*continued*)

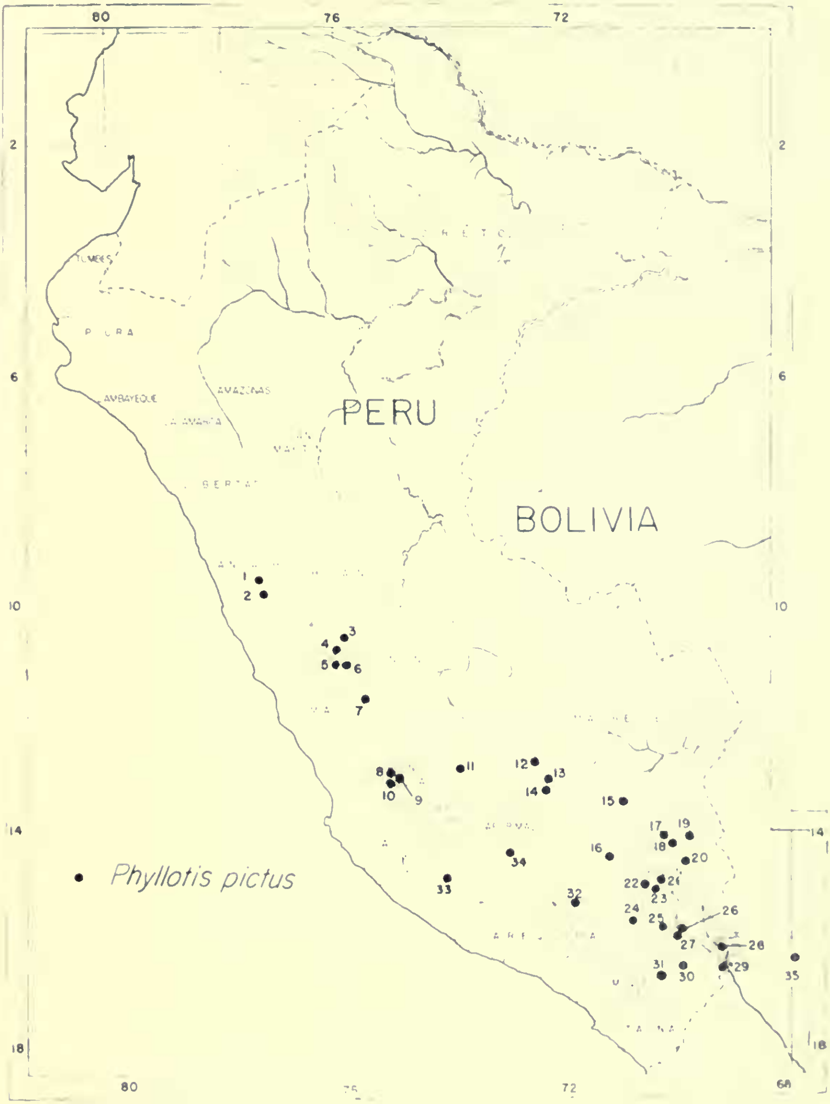
7. Pachacayo, Junín.—C. H. T. Townsend at 12,000 feet.
8. Lachocc, Huancavelica.—A. R. G. Morrison at 12,500 feet.
9. Yaurichucchu, Huancavelica.—C. Kalinowski at 4200 meters.
10. "San Jenaro," Santa Inés, Huancavelica.—C. Kalinowski at 4760 meters.
11. Polanco, Tambo, Ayacucho.—C. Kalinowski.
12. Occobamba Pass, Cusco.—E. Heller at 12,500-13,000 feet.
13. Ollantaytambo, Cusco.—E. Heller at 13,000 feet.
14. Huaracondo, Cusco.—E. Heller at 11,000 feet.
15. Ccolini, Marcapata, Cusco.—C. Kalinowski at 3900 meters.
16. La Raya Pass, Cusco.—E. Heller at 14,000 feet.
17. Puerto Arturo, Puno.—C. C. Sanborn at 13,750 feet.
18. Crucero, Puno.—H. H. Keays at 15,000 feet; P. O. Simons.
19. Limbani, Puno.—C. C. Sanborn at 11,000 feet.
20. Picotani, Puno.—C. C. Sanborn at 14,000 feet.
21. Posoconi, Puno.—C. C. Sanborn at 13,500 feet.
22. San Antonio, Puno.—H. H. Keays at 12,600 feet.
23. Tirapata, Puno.—H. H. Keays at 16,000 feet.
24. Santa Lucía, Puno.—M. R. Portugal.
25. Occomani, Puno.—E. Zúñiga at 12,700 feet.
26. Chuquito, Puno.—C. C. Sanborn at 12,600 feet.
27. Collacachi, Puno.—C. C. Sanborn at 12,800 feet.
28. Yunguyo, Puno.—C. C. Sanborn at 13,000 feet.
29. Huacullani, Puno.—C. C. Sanborn at 12,700 feet.
30. Pairumani, Puno.—O. P. Pearson at 13,000 feet.
31. Santa Rosa, Puno.—O. P. Pearson at 14,000 feet.
32. Cailloma, Arequipa.—C. C. Sanborn and J. M. Schmidt at 14,500 feet.
32. San Ignacio, Arequipa.—13,500 feet.
33. Puquio, Ayacucho.—13,500 feet.
34. Chalhuanca, Apurimac.—14,500 feet.

BOLIVIA

35. Pongo, La Paz.—G. H. H. Tate at 12,000 feet.

ADDITIONAL RECORDS FOR PERU LISTED BY PEARSON (1958, p. 449)

Sibayo, Arequipa, 11,500 feet.
Can-can, Junín.
Galera, Junín, 15,800 feet.
Hacienda Atocsaico, Junín, 13,500 feet.
Maraynioc, Junín, 15,000 feet.
Tarma, Junín, 10,100 feet (CNHM).
Ninacaca, Pasco, 13,500 feet.
Arapa, Puno, 12,600 feet.
Cotacollo, Platería, Puno.
Hacienda Calacala, Puno, 13,000 feet.
Hacienda Chacayani, Puno, 13,200 feet.
Juliaca, Puno, 12,600 feet.
Mazocruz, Puno, 13,000 feet.
Potone, Puno, 15,800 feet.
Puerto Arturo, Puno, 13,000 feet (CNHM).
Puno, Puno, 12,500 feet.
Santa Rosa de Juli, Puno, 14,000 feet.
Tincopalca, Puno, 13,500 feet.
Vilque, Puno.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TUMBES
PIURA
LAMBAYEQUE
AMAZONAS
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AREQUIPA
● Phyllotis pictus

FIG. 92.—Collecting localities of the subspecies of *Phyllotis pictus*. See page 401 for explanation.

Phyllotis pictus Thomas

Reithrodon pictus Thomas, 1884, Proc. Zool. Soc. London, **1884:** 457, pl. 43, fig. 2 (animal), pl. 44, fig. 19 (hind foot), figs. 20–21 (skull). Thomas, 1897, Ann. Mag. Nat. Hist., (6), **20:** 550 (in text). Thomas, 1900, op. cit., (7), **6:** 469—Simons' Cailloma and Arequipa collection.

Rhithrodon [sic] *pictus*, Thomas, 1893, Proc. Zool. Soc. London, **1893:** 337—PERU: *Junín* (San Blas).

E[*uneomys*] *pictus*, Thomas, 1901, Ann. Mag. Nat. Hist., (7), **8:** 254—classification.

E[*uneomys*] (*Auliscomys*) *pictus*, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17:** 143—classification.

Euneomys (*Auliscomys*) *pictus*, Thomas, 1920, Proc. U. S. Nat. Mus., **58:** 232—PERU: *Cusco* (Huaracondo; Ollantaytambo; Occobamba Pass; La Raya Pass).

Auliscomys pictus, Thomas, 1926, Ann. Mag. Nat. Hist., (9), **17:** 317—PERU: Junín. Thomas, 1927, op. cit., (9), **19:** 550—selection of lectotype.

[*Phyllotis* (*Auliscomys*)] *pictus*, Osgood, 1915, Field Mus. Nat. Hist., Zool. Ser., **10:** 191—type of subgenus *Auliscomys*. Osgood, 1947, Journ. Mammal., **28:** 172—characters.

Phyllotis (*Auliscomys*) *pictus*, Sanborn, 1950, Mus. Hist. Nat., "Javier Prado," (A), Zool., no. 5: 6—BOLIVIA: *La Paz* (Pongo); PERU: *Junín* (Carhuamayo; Pachacayo); *Huancavelica* (Lachocc); *Cusco* (Ollantaytambo; Huaracondo); *Puno* (Limbani; Puerto Arturo; Picotani; Posoconi; Chuquito; Collacachi; Occomani; Santa Lucía; Yunguyo; Huacullani); *Arequipa* (Cailloma). Pearson, 1951, Bull. Mus. Comp. Zool., **106:** 146—PERU: *Puno* (Pairumani; Santa Rosa).

Phyllotis pictus Sanborn, 1950, Mus. Hist. Nat., "Javier Prado," (A), Zool., no. 5: 6—*decoloratus* Osgood a synonym. Pearson, 1958, Univ. California Publ. Zool., **56:** 448—BOLIVIA: *La Paz;* PERU: *Ancash; Apurimac; Arequipa; Ayacucho; Cusco; Huancavelica; Junín; Pasco; Puno.*

Phyllotis boliviensis, J. A. Allen (not Waterhouse), 1901, Bull. Amer. Mus. Nat. Hist., **14:** 44—PERU: *Puno* (Tirapata; San Antonio).

Phyllotis (*Auliscomys*) *decoloratus* Osgood, 1915, Field Mus. Nat. Hist., Zool. Ser., **10:** 191—PERU: *Puno* (type locality, Tirapata, 3860 meters altitude). Thomas, 1920, Proc. U. S. Nat. Mus., **58:** 232—doubtfully distinct from *pictus*.

Type.—Male, in spirits, skull separate, British Museum (Natural History) no. 85.4.1.34; collected by C. Jelski; (lectotype selected by Thomas, 1927, supra cit.).

Type locality.—Junín, Junín, Peru; altitude about 4300 meters above sea level.

Distribution (figs. 57, 92).—Highlands of Peru and Bolivia, from the department of Ancash, Peru, south into the department of La Paz, Bolivia; altitudinal range from approximately 3400 to 4700 meters above sea level and possibly higher, to limits of perpetual snow. The locality "San Blas, Cordillera, 18,000 feet [=5600 m.]" recorded for the species by Thomas (1893, p. 337) is almost certainly the San Blas west of Lake Junín on the Junín to Huallay road, altitude about 4000 meters.

External characters.—Size as in the larger species of *Phyllotis;* bicolor tail less than equal but more than one-half combined head and body length, tip not conspicuously tufted; hind feet comparatively short, upper surface gray more or less washed with ochraceous, plantar pads normal, soles finely scutulated (fig. 3); ears small, inner posterior surface ochraceous, pale postauricular tufts usually present; head and, usually, shoulders grizzled, contrasting with brownish back and sides of trunk; rump, base of tail and outer sides of thighs with more tawny or ochraceous than back; prominently projecting guard hairs of rump tipped black, or brown to pure white; ochraceous lateral line not always well defined, frequently interrupted in mid portion; underparts gray to dirty white with dark basal portions of hairs showing through; a small ochraceous pectoral streak sometimes present.

Cranial characters (figs. 58-60, 93).—Supraorbital region of skull narrow, the sides concave or parallel-sided, edges square or slightly raised, never ridged or beaded; zygomata moderately expanded or nearly parallel-sided, their greatest breadth approximately equal to, usually greater than, distance between posterior tips of nasals and anterior border of supra-occipital; anterior border of zygomatic plate plane, slightly concave or slightly convex, the upper anterior corner rounded or pointed but not produced as a spinous process; interparietal well developed; pitted posterolateral palatal excavations usually large and deep; bullae little inflated, their antero-posterior length, less tubes, shorter than alveolar length of molar row; outer side of mandible without capsular projection for encasing base of incisor.

Dental characters (fig. 67,*e*).—Incisors moderately heavy, generally orthodont, varying from slightly opisthodont to slightly proodont, the anterior face of each marked by weakly defined grooves with the outermost barely visible to the unaided eye. Molar rows parallel-sided or slightly divergent posteriorly; upper and lower first molars 4-rooted; molars sub-hypsodont; unworn crowns of upper molars slightly terraced and tending to laminate, little to moderately worn crowns plane and tending to involution and development of a modified sigmoid pattern; cusps more or less ovate in outline and, in

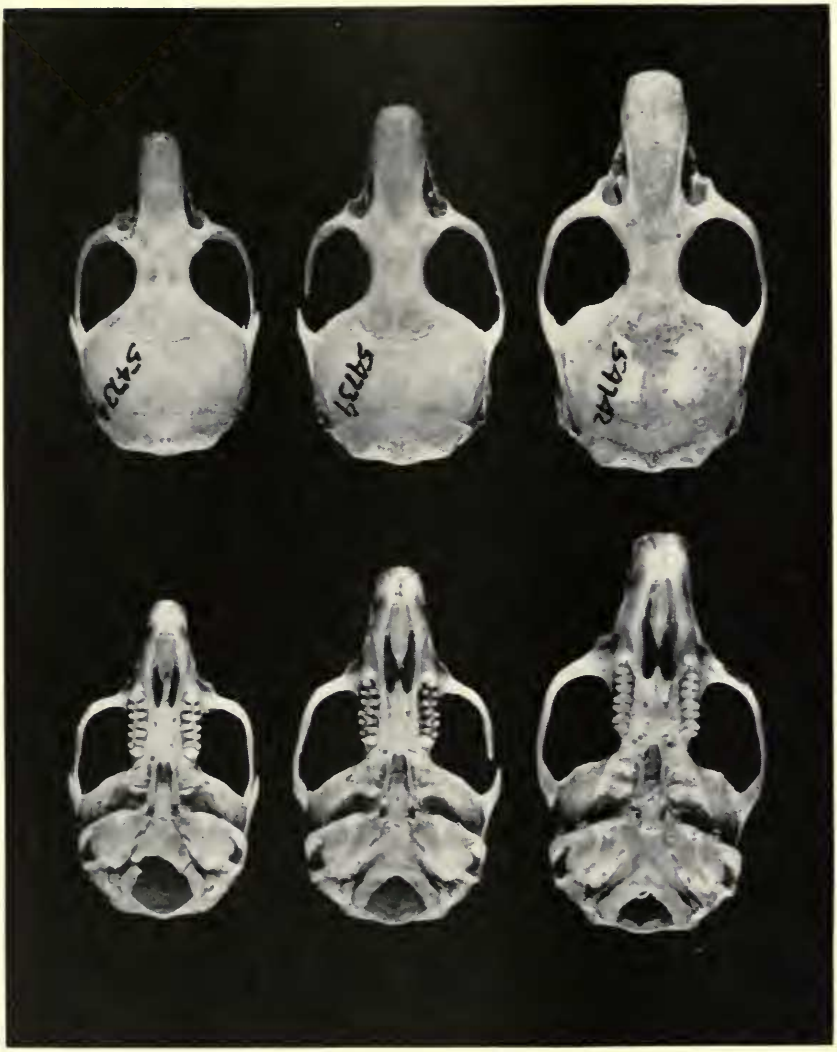


FIG. 93.—*Phyllotis pictus.* Dorsal and ventral aspects of skull, showing variation in size. (Slightly more than × 1½.)

unworn or slightly worn teeth, with a forward flexion; procingulum of $m^{\underline{1}}$ biconulate in unworn, uniconulate and ovate in outline in slightly to extremely worn tooth; procingulum of $m^{\underline{2}}$ well developed, the first primary fold persistent in all but considerably worn tooth; minor fold of $m^{\underline{2}}$ obsolete or poorly developed; vestigial mesoloph often present in $m^{\underline{1-2}}$; postcingulum of $m_{\overline{2}}$ relatively well developed, of m_3 weak; first minor fold of m_2 persistent in well worn tooth; crown pattern of m_3 sigmoid.

Comparisons.—*Phyllotis pictus* is distinguished from the sympatric species *sublimis* and *boliviensis* by generally more saturate coloration, by relative length of tail, hind foot and ear; from dark representatives of the *Phyllotis darwini* complex of the same geographic area, by lax pelage, ochraceous base of tail, grizzled head contrasting with brownish trunk, unpencilled tail less pilose, less sharply bicolor, and consistently shorter than combined head and body length. *Phyllotis micropus*, the only other species comparable in size and appearance is allopatric, more or less uniformly dark brown, and without the markedly contrasting colored portions of the body that distinguish *P. pictus*.

Cranially, *pictus* differs from *boliviensis* chiefly by smaller bullae, from *sublimis* by overall larger size, from the *P. darwini* complex by more widely expanded zygomatic arches, more angular braincase. Molars of *pictus* show the same tendency, though to a lesser degree, for forward flexion of the cusps, noted in *Phyllotis micropus*. Otherwise, the cheek teeth are like those of other species of the genus characterized by well developed procingulum and persistent first primary fold in m^2. Minor fold of m^2 is also persistent in *pictus* except in the extremely worn tooth.

Variation.—In this, and other species of *Phyllotis*, there are the usual intergrading dark and pale color phases. The well-marked grizzled anterior portion of the body may be restricted to the muzzle or may extend over head and anterior half of trunk; in some specimens this area may be marked by large whitish patches. As in *Phyllotis darwini*, a pectoral streak is sometimes present, but there is no consistent relationship between the marking and position of the posterolateral palatal pits. In a series of 11 specimens from Tambo Polanco, Ayacucho, 5 show the pectoral streak but with the posterolateral palatal pits ranging in position from behind, to in front of, the posterior border of the bony palate. Position of the pits in the remaining, unmarked, individuals is similarly variable. A trio of specimens from two localities (Quilcayhuanca; Hacienda Catac) in the department of Ancash, with rump and base of tail hardly differentiated from back, are darkest of the species. Grooving of their incisors is hardly visible to the unaided eye. The two specimens from Quilcayhuanca are extremely old. A skin only from Limbani, Puno, a locality in Amazonian drainage, agrees with Puno material from the Lake Titicaca basin except that the upper surface of its hind foot is nearly uniformly ochraceous. A young individual from Puerto Arturo, Puno, near the Amazonian side of the divide, shows nearly as much ochraceous. The same character appears in specimens from Junín and Cailloma. A subadult from Pongo, Bolivia, Amazonian drainage, is indistinguishable from the young Puerto Arturo individual. In contrast, specimens of *Phyllotis osilae* from the same areas in the Lake Titicaca and the Amazonian drainage, represent, respectively, the well-marked subspecies, pale *P. osilae osilae* and blackish *P. osilae phaeus*.

Habitat and habits.—The following account is from Pearson (1951, p. 146): "*A*[*uliscomys*] *pictus* seems to prefer grassy places, especially those near water, but it also lives in stone walls and in places far from water. One was caught in an unoccupied Indian hut in which *Akodon jelskii pulcherrimus* was also living, but its usual associates are *Akodon boliviensis* and *A. amoenus*. It is active day and night. I was unable to distinguish between the skull fragments of *pictus* and *sublimis* in the Pairumani owl pellets, but these two species combined provided the owls with 54 of their 153 meals. By weight, this would be the most important item in the diet of the owls.

"None of the females caught between July 14 and 30 at Pairumani and Santa Rosa were pregnant, and none of the 8 males had testes larger than 4 mm. A specimen in greyish juvenile pelage caught on December 22 suggests that breeding begins in September or October as in many of the other species of mice in the region. The ratio of sexes was 17 males to 16 females."

A female taken April 13, 1915 by Edmund Heller in Huaracondo, Cusco, Peru, is labelled as having been gravid with 5 embryos.

Taxonomy.—*Auliscomys* Osgood was proposed as a subgenus of *Phyllotis* to contain *pictus* Thomas (type), *boliviensis* Waterhouse, and *sublimis* Thomas. The original definition of *Auliscomys* was based on a comparison of *pictus* with *Phyllotis darwini* and *Euneomys* and does not apply in every case to included species *boliviensis* and *sublimis*. The upper incisors in *Auliscomys*, said to be marked by "slight but distinct grooves," refers to *pictus* but not always to *boliviensis* and *sublimis*. The greater hypsodonty attributed to *Auliscomys* as compared with *P. darwini*, is not confirmed in present material. Retention in m^2 of the first primary fold ascribed by Osgood (in different terminology) to *Auliscomys*, serves to distinguish *pictus* and *boliviensis* from some members of the *P. darwini* complex but not from other species of the genus *Phyllotis*. Later,

TABLE 54. — Measurements of *Phyllotis pictus* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
Quilcayhuanca	133,138	102,107	28,28	22,22	30.2,31.5	16.9,17.0	5.6,5.8
Catac	135	81	25	21	30.2	17.5	5.4
Junín[1]	100	75	24.1	18.8	28.0	17.0	5.6
Junín	128(114–138)7	92(85–95)7	26.5(26–27)7	—	30.6(30.0–31.4)4	17.0(16.8–17.5)4	5.6(5.4–5.9)7
Carhuamayo	129,134,147,147	86,93,100,97	28,28,28,27	—,—,—,—	29.9,30.1,32,33	17.3,17.3,—,18.9	5.7,5.8,5.5,5.7
Lachocc	116,121	95,97	25,23	21,23	30.8,30.8	18.0,17.8	5.6,5.8
Santa Inéz	134	76	28	23	31.7	18.1	6.1
Yaurichucchu	122	89	26	23	30.3	17.4	5.9
Polanco	134(122–140)11	97(85–104)11	27(26–28)11	21(20–22)11	30.7(29.3–31.7)11	17.1(16.0–17.8)11	5.7(5.5–5.9)11
Huaracondo	123	93	26	21	29.8	16.6	5.6
Ollantaytambo	125	94	26	20	30.0	17.3	5.4
Ccolini	108,127	95,98	24,27	21,20	29.6,—	17.3,17.0	5.8,5.5
Cailloma	117(101–132)9	87(77–99)9	25.5(25–26)9	20(19–21)9	29.1(27.8–30.8)9	16.6(15.9–17.2)9	5.5(5.3–5.8)9
Pto. Arturo	124,132	87,93	26,27	—,—	28.8,30.3	16.2,17.0	5.3,5.8
San Antonio	101	76	24	—	28.7	16.6	5.5
Picotani	125(117–132)9	88(83–94)9	26.5(26–27)9	—	29.4(28.0–30.9)9	16.9(16.0–17.9)8	5.5(5.3–5.8)9
Posoconi	115(106–123)5	95(93–97)5	27.5(27–28)5	—	29.3(28.5–29.8)5	16.2(16.1–16.3)5	5.5(5.4–5.6)5
Sta. Lucía	135	76(?)	25	—	29.6	17.0	5.5
Collacachi	127,129,117,127	93,106,118,88	27,27,29,27	—,—,—,—	29.0,30.1,30.2,30.3	16.8,17.1,17.1,17.1	5.3,5.3,5.2,5.6
Chuquito	111	90	28	—	28.4	16.0	5.4
Yunguyo	135(122–143)5	87(84–90)5	27(25–28)5	—	30.0(29.0–31.7)5	16.8(16.4–17.7)4	5.6(5.4–5.8)5

[1] Type, from original description.

Thomas (1916a, p. 143) reclassified *Auliscomys* as a subgenus of *Euneomys*. He distinguished *Auliscomys* by the "mainly vertical" portion of the maxillo-premaxillary suture from *Euneomys* in which the suture is "bowed forward below." The same character separates *Phyllotis* from *Euneomys* and Thomas proved nothing by the transfer of *Auliscomys*. Thomas modified his views later (1926a, p. 317) and proposed that *Auliscomys* and other subgenera of *Euneomys*, be treated as full genera. This arrangement, he averred, was "far more convenient both for labelling and reference." Osgood (1947, p. 172) with more concern for biological realities restored *Auliscomys* to the genus *Phyllotis*.

Basing comparisons on a single topotype of true *pictus*, Osgood first described *Phyllotis* (*Auliscomys*) *decoloratus* as "smaller and paler" than the single topotype of *P. pictus* with which it was compared. Additional material has shown these characters to be illusory. The type of *decoloratus*, judged by measurements, is a juvenal, and all but one of the remaining 10 specimens of the original series of *decoloratus* (Tirapata, 4; San Antonio, 5; Crucero, 1) are juvenals and subadults.

Measurements.—See Table 54.

Specimens examined.—127. BOLIVIA.—*La Paz:* Pongo, 1 (AMNH). PERU.—*Ancash:* Quilcayhuanca, 2 (CNHM); Hacienda Catac, Ticapampa, 1 (CNHM); *Junín:* Junín, 11 (CNHM); Carhuamayo, 9 (CNHM); near Junín, 2 (CNHM); Chipa, 3 (AMNH). *Huancavelica:* Lachocc, 2 (CNHM); "San Jenaro," Santa Inéz, 4 (CNHM); Yaurichucchu, 1 (CNHM). *Ayacucho:* Polanco, Tambo, 11 (CNHM); *Cusco:* Huaracondo, 1 (CNHM); Ollantaytambo, 2 (CNHM); Ccolini, Marcapata, 2 (CNHM). *Arequipa:* Cailloma, 19 (CNHM). *Puno:* Limbani, 1 (CNHM); Puerto Arturo, 3 (CNHM); San Antonio, 5 (AMNH); Tirapata, 4 (AMNH); Crucero, 1 (AMNH); Picotani, 10 (CNHM); Posoconi, 12 (CNHM); Santa Lucía, 1 (CNHM); Occomani, 4 (CNHM); Hacienda Collacachi, 6 (CNHM); Chuquito, 1 (CNHM); Yunguyo, 6 miles S, 6 (CNHM); Huacullani, 2 (CNHM).

Phyllotis boliviensis Waterhouse. (Synonymy under subspecies.)

Distribution (figs. 57 and 94).—The *altiplano* of southern Peru, northern Chile, and northwestern Bolivia; altitudinal range from approximately 3500 meters above sea level to near limits of perpetual snow.

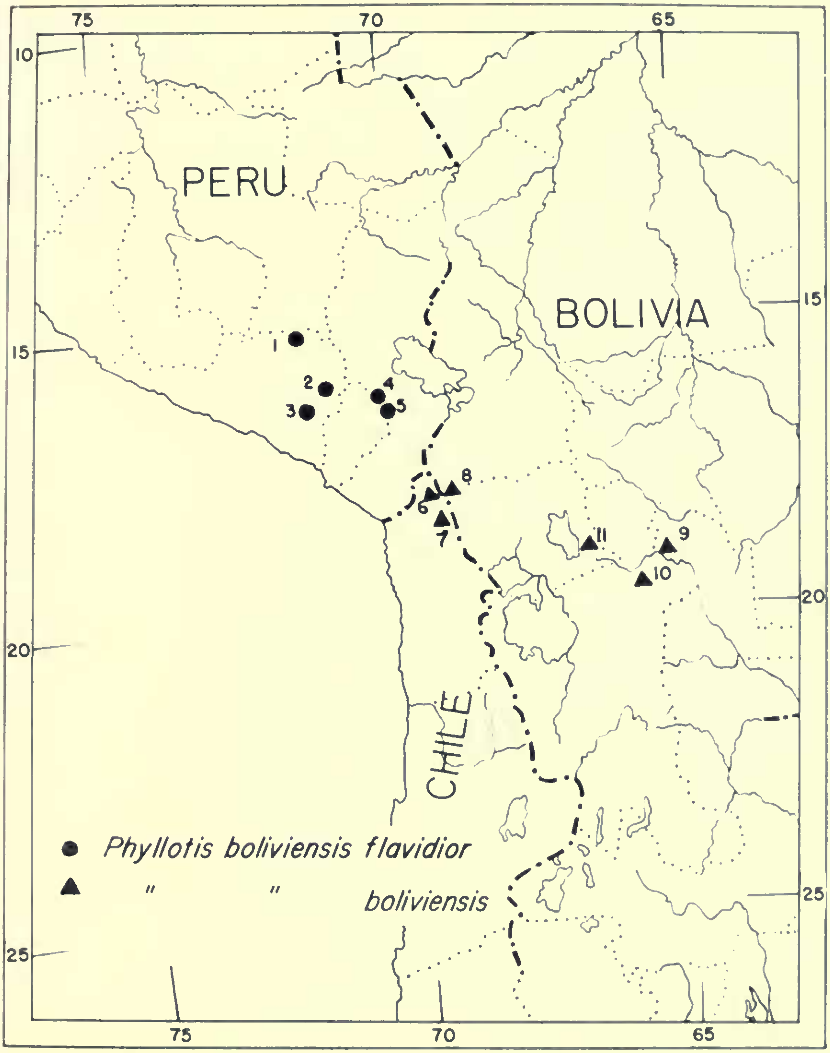

75
70
65
10
15
20
25
PERU
BOLIVIA
CHILE
1
2
3
4
5
6
7
8
9
10
11
● Phyllotis boliviensis flavidior
▲ " " boliviensis

FIG. 94.—Collecting localities of the subspecies of *Phyllotis boliviensis*. See explanation below.

EXPLANATION OF FIGURE 94

Phyllotis boliviensis: collecting localities and collectors.

Type localities in **boldface**.

Phyllotis boliviensis flavidior (1–5)

PERU

1. **Bateas, Cailloma, Arequipa.** B. Hunt at 4500 meters.
1. Cailloma, Arequipa.—C. C. Sanborn and J. M. Schmidt at 14,500 feet; P. O. Simons.

External characters.—Moderately large; tail from one-half to nearly as long as combined head and body length, its upper surface ochraceous with terminal portion darker, underside whitish or buffy basally becoming ochraceous terminally, tip untufted; hind foot comparatively large and strongly developed, upper surface gray or buffy, an ochraceous metatarsal patch often present, plantar pads normal, soles coarsely granulated; large ears with prominent ochraceous preauricular tufts and smaller whitish or buffy postauricular tufts; upper surface of head and body with coarse mixture of gray, brown, and buff or ochraceous, sides paler, muzzle whitish; ochraceous lateral line not always well developed; underparts whitish or pale gray, more or less washed with buff; an ochraceous pectoral streak sometimes present.

Cranial characters (figs. 59, 60, 95).—Skull more angular, less elongate than in other *Phyllotis;* supraorbital region as in *P. pictus,* zygomata more bowed, their breadth approximately equal to, or greater than, distance between posterior tips of nasals and anterior border of supraoccipital; anterior border of zygomatic plate more or less plane, never markedly concave, the anterior corner usually rounded, sometimes pointed but not produced; interparietal better developed, especially longitudinally, than in *P. pictus;* bullae well inflated, thin-walled, their antero-posterior length, less tubes, subequal to alveolar length of molar row; distance across mastoid processes in fully adult specimens approximately one-half or more greatest skull length; outer side of mandible without projecting capsule for encasing base of incisor.

Explanation of Figure 94 (*continued*).

2. Salinas, Arequipa.—C. C. Sanborn at 14,100 feet.
3. Arequipa, Arequipa.—P. O. Simons.
4. San Antonio de Esquilache, Puno.—C. C. Sanborn at 15,000 feet.
5. Caccachara, Puno.—O. P. Pearson at 16,000 feet.

Phyllotis boliviensis boliviensis (6–11)

CHILE

6. Puna de Tarapacá, Tarapacá.—G. Mann.
7. Choquelimpié, Tarapacá.—C. C. Sanborn at 15,000 feet.

BOLIVIA

8. Esperanza, Pacajes, La Paz.—F. Steinbach at 4200 meters.
9. Chuquisaca=Sucre, Chuquisaca.—Castelnau and Deville Expedition.
10. **Potosí, Potosí** (3945 meters).—T. Bridges; P. O. Simons.
11. Livichuco, Oruro.—P. O. Simons at 4500 meters.

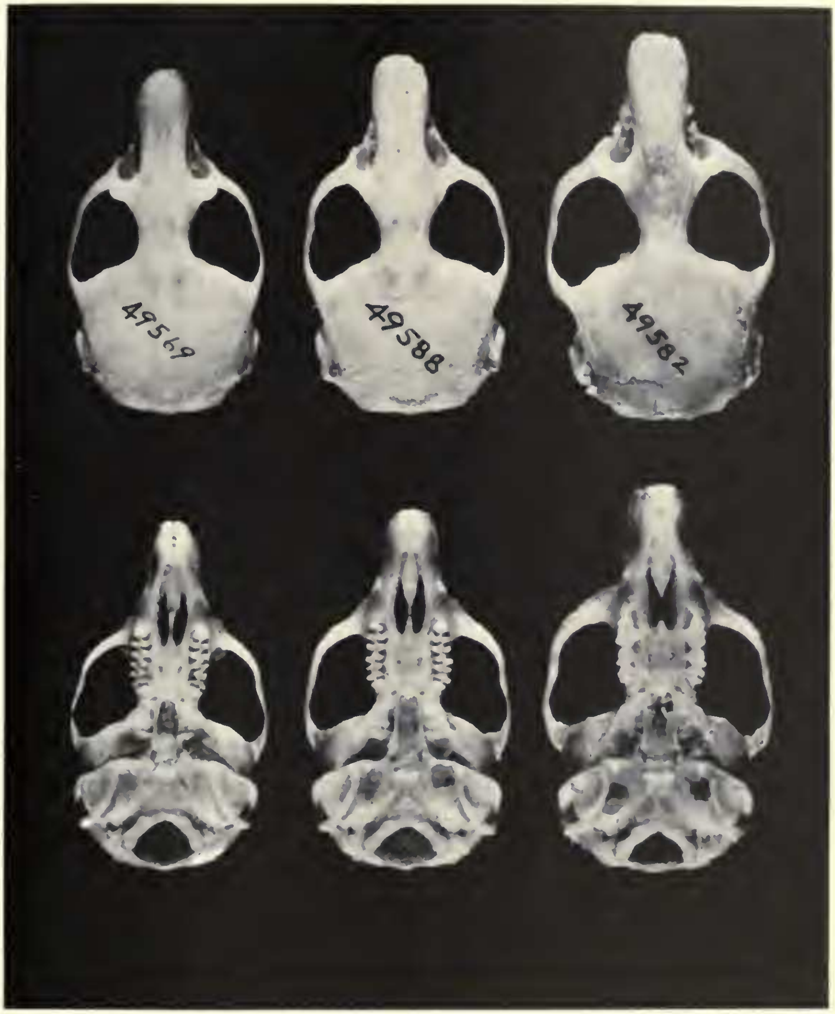


FIG. 95.—*Phyllotis boliviensis*. Dorsal and ventral aspects of skulls, showing variation in size. (Slightly more than × 1½.)

Dental characters (fig. 96).—Incisors generally proodont, sometimes orthodont, their anterior face smooth or marked by faint shallow striae usually not visible to the unaided eye. Molar rows parallel-sided or slightly bowed; upper first molar with 3 or 4 roots, lower 3-rooted; hypsodont crowns plane or very slightly terraced in unworn upper molars, more persistently terraced in lower molars; unworn or slightly worn crowns involuted, outline of cusps more or less

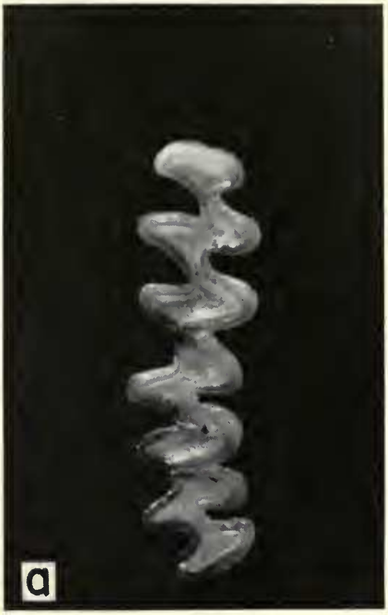
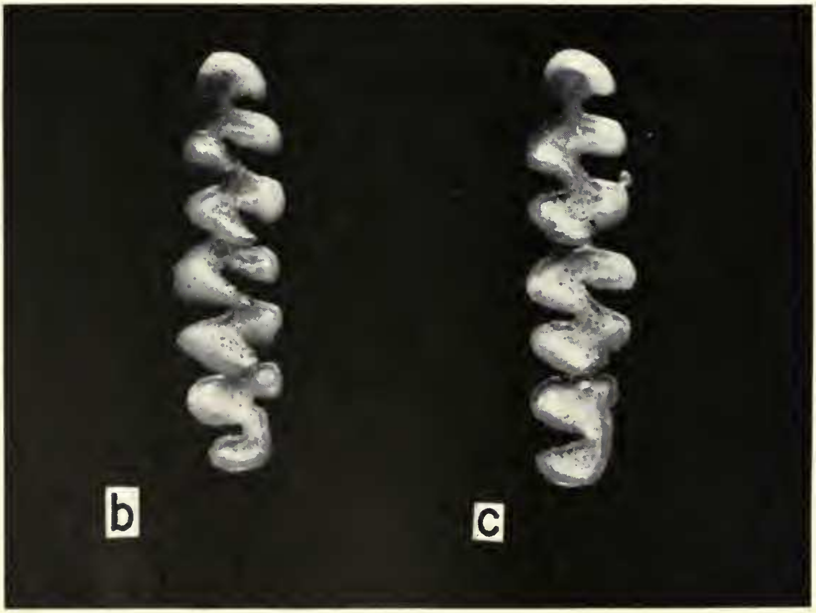


FIG. 96.—*Phyllotis boliviensis.* *a*, right upper molars; *b*, moderately worn left lower molars; *c*, well worn left lower molars.



ovate; modified sigmoid pattern of moderately worn m^2 becoming 8-shaped with increased wear; procingula of m^{2-3} well developed, the first primary folds persistent in all but extremely worn teeth; minor fold of m^2 not developed; vestigial mesolophs often present in m^{2-3}; postcingulum of m_2 well developed, of m_3 reduced; minor fold of m_2 absent in moderately worn tooth.

Comparisons.—In pale coloration, *Phyllotis boliviensis* resembles sympatriots *P. sublimis* and *P. darwini rupestris*. It is separable from *P. darwini* (and *P. osilae*) by shorter, untufted, less completely bicolor tail, bright preauricular tufts, and, in some populations, by the ochraceous metatarsal patch. Superficial distinction from *sublimis* is made by greater size, proportionately longer tail and other characters given in the descriptions. The proodont and practically smooth-faced incisors of *boliviensis* distinguish it from all other species of *Phyllotis;* molars generally as in *pictus,* but cusps not flexed forward, minor folds of m^2 more reduced, anterior cingulum of m^3 and vestige of mesoloph larger, anterior fold of m_1 obsolete.

Variation.—Most variation in color is the result of molt. Old grizzled pelage of head and shoulders is defined by a molt line. Old pelage mid-dorsally appears as a gray or plumbeous band. Molt area on rump converges to a concentric line. Condition of pelage in a series of 22 specimens from Bolivia taken from October 9 to November 15 ranges from prime to extremely old. A series collected in Cailloma, Peru, in August, also includes individuals in old and new pelage, but in molting individuals the mid-dorsal area is gray not plumbeous as in the Bolivian mice. A more or less well-defined pectoral streak is present in many individuals. No relationship between this marking and cranial characters is apparent.

Posterolateral palatal pits of each side are usually paired, with one situated anteriad of median posterior border of palate, the other anteriad or posteriad of border.

Remarks.—Because of its greater angularity, the dorsal outline of the skull of *P. boliviensis* more nearly resembles that of microtines than do skulls of other species of the genus *Phyllotis.*

Habitat and habits.—According to Pearson (1951, p. 145), who observed the mammals of the Lake Titicaca region in Puno, Peru, the species "lives at high altitudes in many kinds of habitats, such as rock slides, stone walls, and even in abandoned tuco-tuco [*Ctenomys*] burrows out in open country. Its food must also be varied, for twice it was seen feeding on lichens in rocky places, yet no lichens were available to those living in the tuco-tuco diggings. It is chiefly diurnal. . . . We saw many during the day, and a few were trapped at night. The owls at Pairumani caught none, which confirms the evidence that these mice are chiefly diurnal. Because they live in so many kinds of places, their animal associates include most of the species living at high altitudes. Most remarkable, however, is their close relationship with viscachas. I found them living in the midst of a colony of viscachas, and two of these *Auliscomys* [i.e., *Phyllotis boliviensis*] habitually sunned on the rocks within a foot or two of sunbathing viscachas. When the viscachas moved down out of the rocks to feed, *Auliscomys* went along, too, and grazed like an elf among grownups. I have seen an *Auliscomys* that was feeding beside a viscacha scurry for shelter when a distant viscacha sounded the alarm whistle. The nearby viscacha in this case did not retreat. The nervous, droll movements of these *Auliscomys* are always entertaining, sometimes startling. Instead of peering cautiously out of tuco-tuco burrows, they pop out, ears, head and shoulders, with paws folded neatly on their breasts."

Regarding the breeding among these mice, Pearson (op. cit. p. 146) observed that "a male at Pairumani on July 19 had small testes, several males at Caccachara had large testes (up to 10 mm. long) after September 15, and at Cailloma on December 6. The number of embryos varied from three to four. Juvenile individuals were seen on November 7 and 20."

The type specimen of *boliviensis* was described by its collector, Thomas Bridges (*in* Waterhouse, supra cit.) as a "charming little animal . . . found in the same locality as the above ["*Ctenomys Braziliensis*"], inhabiting the abandoned caves of the former species. It makes its appearance in the afternoon, when the sun is nearly on the horizon, to feed on grass, and is often seen sitting on its hind legs; and it then presents its pretty white abdomen and erect ears. In this position it has the appearance of a rabbit in miniature. The natives call it 'Achohalla,' pronounced 'Ha-cho-ha-ya'." This remarkably tame mouse not only permits itself to be observed at close range but also, according to Mann (1945, p. 81) does not attempt to bite when captured, is gentle when handled and fearlessly accepts food from its captor.

Phyllotis boliviensis boliviensis Waterhouse

Hesperomys Boliviensis Waterhouse, 1846, Proc. Zool. Soc. London, **1846:** 9. Waterhouse, 1846, Ann. Mag. Nat. Hist., (1), **17:** 483. Gervais, 1855, Castelnau Exped. Amérique Sud, pt. 7, Zool., Mamm., p. 111—BOLIVIA: *Chuquisaca* (Chuquisaca [=Sucre]).

H[esperomys (Phyllotis)] boliviensis, Thomas, 1884, Proc. Zool. Soc. London, **1884**: 449—classification.

[Phyllotis] boliviensis, Trouessart, 1897, Cat. Mamm., p. 534—classification.

Phyllotis boliviensis, Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9**: 223—BOLIVIA: *Oruro* (Livichuco); *Potosí* (Potosí). Thomas, 1902, op. cit., (7), **10**: 249—BOLIVIA: *Potosí*. Mann, 1945, Biológica, Trab. Inst., Biol. Univ. Chile, fasc. 2: 78, figs. 29, 30, 31, 36, pls. 29, 30—CHILE: *Tarapacá* (Puna).

Euneomys (Auliscomys) boliviensis, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 143—classification.

[Phyllotis (Auliscomys)] boliviensis, Osgood, 1915, Field Mus. Nat. Hist., Zool. Ser., **10**: 191—classification.

Phyllotis (Auliscomys) boliviensis, Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 210, fig. 29 (skull)—part, CHILE: Tarapacá (Choquelimpié). Sanborn, 1950, Mus. Hist. Nat. "Javier Prado," (A), Zool., no. 5: 9—BOLIVIA: *La Paz* (Esperanza); CHILE: *Tarapacá* (Choquelimpié).

Phyllotis boliviensis boliviensis, Pearson, 1958, Univ. California Publ. Zool., **56**: 452—BOLIVIA: *La Paz* (Esperanza); *Oruro* (Livicucho [=Livichuco?]); *Potosí* (Potosí; Potosí Peak); CHILE: *Tarapacá* (Choquelimpié).

[Hesperomys (Hesperomys)] Waterhousii Trouessart, 1881, Bull. Soc. d'études Sci. d'Angers, **10**, (1): 138—new name for *boliviensis* Waterhouse, a secondary homonym of *Akodon boliviensis* Meyen.

[Phyllotis] Waterhousii, Trouessart, 1897, Cat. Mamm., p. 534—a synonym of *Phyllotis boliviensis* Waterhouse.

Type.—Adult, skin and skull, British Museum (Natural History) no. 45.11.18.9; collected by Thomas Bridges.

Type locality.—"A few leagues south of Potosí, at an elevation of 12,000 feet," Potosí, Bolivia (Bridges, *in* Waterhouse, supra cit., pp. 8-9; see also Thomas, 1902, Ann. Mag. Nat. Hist., (7), **10**: 249).

Distribution (fig. 94).—Highlands of western Bolivia, in departments of Chuquisaca, Potosí, Oruro and La Paz, west into the highlands of Tacna, Peru (no records), and Tarapacá, Chile; altitudinal range from 3750 meters (type locality) to 4700 meters (Choquelimpié, Tarpacá, Chile) above sea level.

Characters.—Those of the species, upper surface of hind foot usually without well-defined ochraceous metatarsal patches.

Remarks.—Specimens here referred to *boliviensis* are from localities about midway between the type localities of *boliviensis* and *flavidior*.

Measurements.—See Table 55.

Specimens examined.—29. BOLIVIA. *La Paz:* Esperanza, Pacajes, 4200 meters, 22 (CNHM). CHILE. *Tarapacá:* Choquelimpié, 4700 meters, 7 (CNHM).

TABLE 55.—Measurements of *Phyllotis boliviensis boliviensis* Waterhouse

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
BOLIVIA				19[2]	—	—	—
Potosí[1]	133	87	28.6	28(25–35)17	30.6(29.5–31.4)10	17.2(16.4–18)9	5.6(5.3–5.9)17
Esperanza	113(105–120)17[3]	94(90–105)17	27(25–30)17				
CHILE							
Choquelimpié	123	88	28	—	29.3	17.4	5.5
”	125	90	28	—	30.5	17.6	6.0
”	126	89	29	—	30.6	17.3	5.6

[1] Type, from original description.

[2] From crown.

[3] Collector's measurement to nearest half centimeter or centimeter.

TABLE 56.—Measurements of *Phyllotis boliviensis flavidior* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
PERU							
Bateas[1]	126	95	24(s.u.)	26	30.5	16.8	5.6
Cailloma	121(111–135)16	92(83–101)16	29(26–31)17	26(25–29)14	30.3(29.0–32.0)15	17.1(16.1–18.1)17	6.0(5.6–6.2)17
Salinas	13.7	78	31	—	32.6	19.1	5.8
S. Antonio	126(112–145)8	95(90–100)8	30(30–31)8	27(26–28)7	30.8(29.5–32.5)7	17.3(16.7–18.5)8	5.8(5.4–6.0)8

[1] Type, from original description.

Phyllotis boliviensis flavidior Thomas

Phyllotis boliviensis, Thomas, 1897, Ann. Mag. Nat. Hist., (6), **20:** 550—in text; PERU: *Puno*. Thomas, 1900, op. cit., (7), **6:** 469—PERU: *Arequipa* (Cailloma; Arequipa).

Phyllotis (Auliscomys) boliviensis, Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30:** 210—part; PERU: *Puno*.

Phyllotis boliviensis flavidior Thomas, 1902, Ann. Mag. Nat. Hist., (7), **10:** 248. Pearson, 1958, Univ. California Publ. Zool., **56:** 452—PERU: *Arequipa* (Cailloma; Huaylarco; Salinas; Sibayo); *Moquegua* (Lago Suche; Pampa Huaitire; Titire); *Puno* (Caccachara; Pairumani; Pampa de Ancomarca; Pampa de Capazo; Pasto Grande; San Antonio de Esquilache).

[*Euneomys (Auliscomys) boliviensis*] *flavidior*, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17:** 143—classification.

[*Phyllotis (Auliscomys) boliviensis*] *flavidior*, Osgood, 1915, Field Mus. Nat. Hist., Zool. Ser., **10:** 191—classification.

Phyllotis (Auliscomys) boliviensis flavidior, Sanborn, 1950, Mus. Hist. Nat. "Javier Prado," (A), Zool., no. 5: 9—PERU: *Arequipa* (Cailloma; Salinas); *Puno* (San Antonio de Esquilache). Pearson, 1951, Bull. Mus. Comp. Zool., **106:** 144—PERU: *Puno*.

Type.—Female, skin and skull, British Museum (Natural History) no. 2.7.2.5, collected 19 May 1901, and presented by Bernard Hunt.

Type locality.—Bateas, about 15 kilometers west of Cailloma, Arequipa, Peru; altitude 4500 meters above sea level.

Distribution (fig. 94).—*Altiplano* of southern Peru in departments of Arequipa and Puno; known altitudinal range from 4400 meters (Salinas, Arequipa) to 5300 meters (Caccachara, Puno) above sea level.

Characters.—Like typical *boliviensis* but with a well-marked metatarsal patch usually present.

Remarks.—In the original description a number of differences in coloration are noted between *boliviensis* and *flavidior*. In present material from three relatively widely separated localities, only the character of the metatarsal patch is valid.

Measurements.—See Table 56.

Specimens examined.—36. PERU. *Arequipa:* Cailloma, 26 (CNHM); Salinas, 1 (CNHM). *Puno:* San Antonio de Esquilache, 9 (CNHM).

Phyllotis sublimis Thomas. (Synonymy under subspecies.)

Distribution (figs. 57, 97).—Highlands of southern Peru in the departments of Ayacucho, Apurimac, Arequipa and Puno, thence

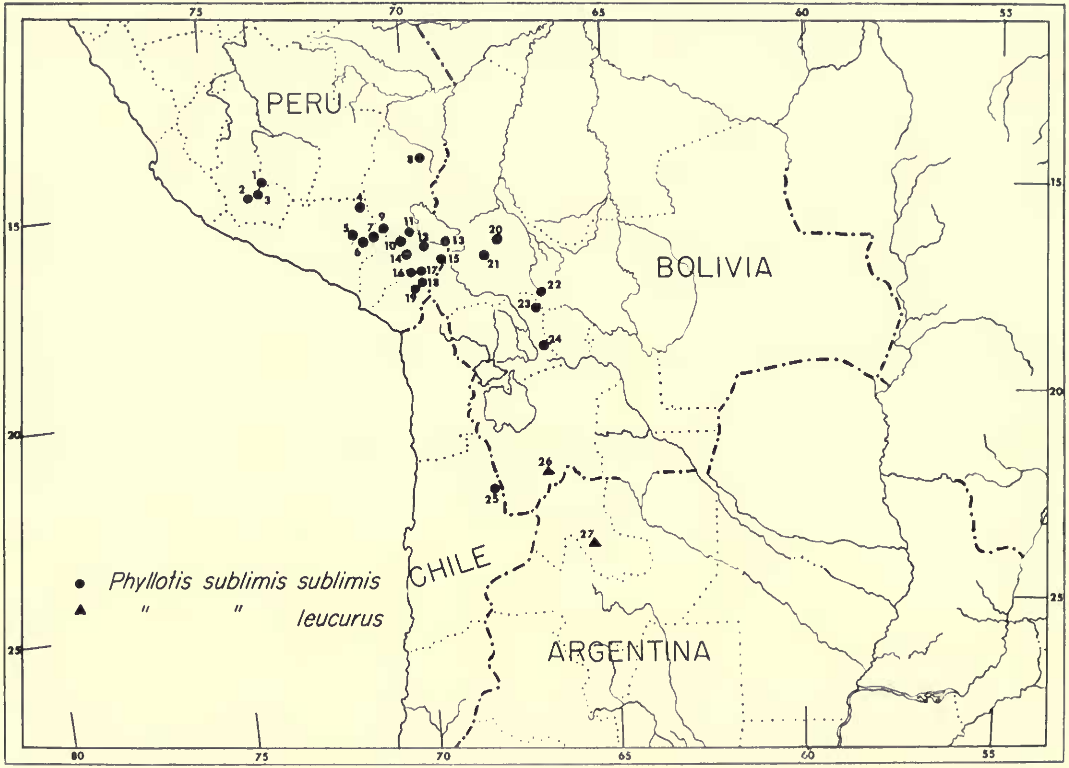

PERU
BOLIVIA
CHILE
ARGENTINA
● Phyllotis sublimis sublimis
▲ " " leucurus
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FIG 97.—Collecting localities of the subspecies of *Phyllotis sublimis*. See opposite page for explanation.

EXPLANATION OF FIGURE 97

Phyllotis sublimis: collecting localities and collectors.

Type localities in **boldface.**

Phyllotis sublimis sublimis

PERU

1. Chalhuanca, Apurimac, 25 miles SW.—O. P. Pearson at 14,500 feet.
2. Puquio, Ayacucho, 9 miles NE.—O. P. Pearson at 14,500 feet.
3. Puquio, Ayacucho, 21 miles ENE.—O. P. Pearson at 14,600 feet.
4. **Rinconado Malo, Arequipa.**—P. O. Simons at 5500 meters.
5. Sumbay, Arequipa.—C. C. Sanborn at 13,500 feet.
6. Salinas, Arequipa.—C. C. Sanborn and J. M. Schmidt at 14,000 feet.
7. Huaylarco, Arequipa.—O. P. Pearson or associates at 15,000 feet.
8. Limbani, Puno.—C. B. Koford at 13,800 feet and 15,000-15,500 feet.
9. Santa Lucía, Puno.—M. R. Portugal, at 13,300 feet.
10. San Antonio de Esquilache, Puno.—C. C. Sanborn at 15,000 feet.
11. Puno, Puno.—Variously collected by O. P. and A. K. Pearson and C. B. Koford at 3.1 miles NE., 13,200 feet; 3.1 miles W., 13,000 feet; 48 miles W., 13,500 feet; 51 miles W., 14,000 feet.
12. Pairumani, Puno.—O. P. Pearson at 13,000 feet.
13. Yunguyo, Puno.—C. C. Sanborn at 12,700 feet.
14. Caccachara, Puno.—O. P. Pearson at 15,500 feet.
15. Huacullani, Puno.—C. C. Sanborn at 12,700 feet.
16. Río Santa Rosa, Puno.—C. B. Koford at 14,400 feet.
17. Mazocruz, Puno.—Specimens from 17 miles S. at 13,500 feet and 30 miles S. and 3 miles W. at 14,300 feet.
18. Pampa de Ancomarca, Puno.—O. P. Pearson at 13,800 feet.
18. Pampa de Capazo, Puno.—Specimens collected at 14,300 feet.
19. Pampa de Titiri, Tacna.—Specimens collected at 14,600 feet.

BOLIVIA

20. El Cumbre, La Paz.—G. H. H. Tate, at 15,200 feet.
21. La Paz, La Paz, 20 miles S.—O. P. Pearson at 13,000 feet.
22. Cosmini, Cochabamba.—P. O. Simons at 4300 meters.
23. Oruro, Oruro, 20 miles NE.—O. P. Pearson at 14,000 feet.
24. Livichuco, Oruro.—P. O. Simons at 4500 meters.

CHILE

25. Toconce, Antofagasta.—K. Koford at 4700 meters.

Phyllotis sublimis leucurus

BOLIVIA

26. Lipez, Potosí.

ARGENTINA

27. La Lagunita, Sierra de Zenta, Jujuy.—E. Budín at 4500 meters.
27. Sierra de Zenta, Jujuy.

south through the highlands of northeastern Chile, western Bolivia and northern Argentina; altitudinal range from 4000 meters above sea level to limits of perpetual snow.

External characters.—Smallest of the short-tailed species of *Phyllotis;* tail from one-third to less than two-thirds combined head and body length, white, gray or buff, with or without a brown mid-dorsal line on upper surface, tip untufted; hind foot proportionately small, well haired above, naked below except on heel, soles smooth or lightly scutulated, plantar pads relatively large; ears not conspicuously large, pale postauricular patches sometimes present; upper surface of head and body buffy finely mixed with black, the anterior portion grizzled, posterior portion, especially rump, more saturate, sides of body paler, cheeks whitish, lateral line usually indistinct or interrupted; underparts sharply defined whitish to pale gray with plumbeous of basal portions of hairs showing through.

Cranial characters (figs. 58–60, 98, 109, 110).—Supraorbital region of skull as in *pictus,* but borders hardly or not at all raised; zygomata more or less evenly bowed, greatest breadth approximately equal, usually more than, distance between posterior tips of nasals and anterior border of supraoccipital; zygomatic plate as in *boliviensis;* interparietal extremely reduced; bullae moderately inflated, their antero-posterior length, less tubes, not equal to alveolar length of molar row; outer side of mandible without capsular projection encasing base of incisor.

Dental characters (figs. 67, 99, 111).—Incisors orthodont or slightly opisthodont, their anterior face nearly always marked by faint, shallow grooves hardly or not at all visible to the unaided eye. Molar rows parallel-sided; upper first molar 4-rooted, lower 3-rooted; subhypsodont crown plane, or slightly terraced in unworn teeth; enamel of crown involuted, forming a modified sigmoid pattern in $m^{\underline{2}}$; outline of cusps subovate; outline of procingulum of $m^{\underline{1}}$ ovate or subcordate; procingulum of $m^{\underline{2}}$ weakly developed, the first primary fold hardly or not at all persistent in worn tooth; procingulum of $m^{\underline{3}}$ reduced; first minor fold of $m^{\underline{2}}$ slightly or not developed; vestige of mesoloph sometimes present in $m^{\underline{1-2}}$; postcingulum of $m_{\overline{2}}$ moderately developed, of $m_{\overline{3}}$ reduced; minor fold well developed and persistent in $m_{\overline{2}}$.

Comparisons.—Small size, pale coloration, thick, soft fur, extremely short, whitish, thinly haired tail, and soles bare except at heel, are external characters that distinguish *Phyllotis sublimis* from all other phyllotine rodents. There is striking superficial resem-

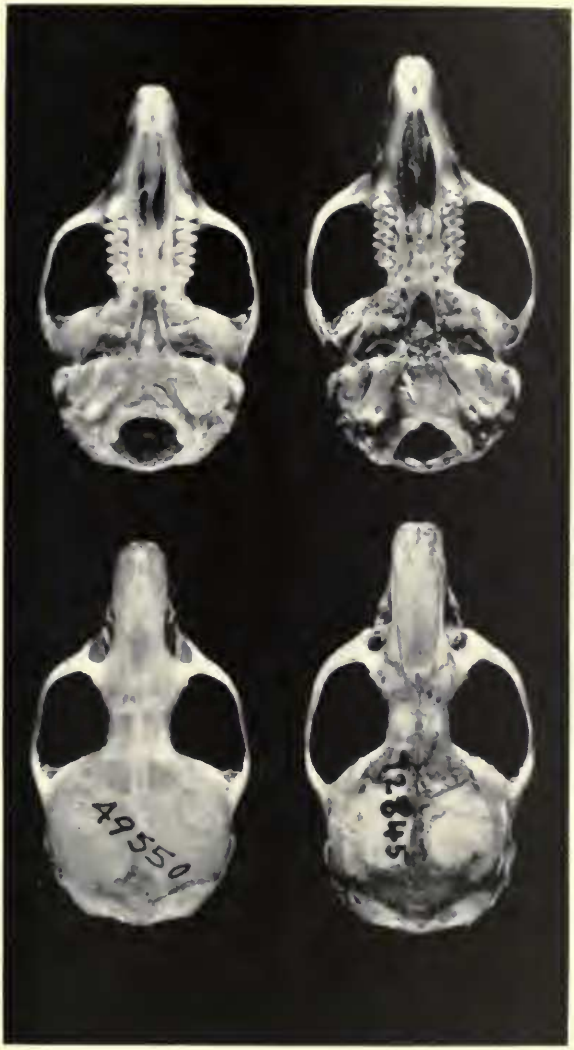


FIG. 98.—*Phyllotis sublimis.* Dorsal and palatal aspects of skull (× 2).

blance between *P. sublimis* and the vole-like *Galenomys garleppi* in size, color, character of pelage and proportional lengths of tail, limbs and ears. The latter is separated from the former by thickly haired tail and soles, arched dorsal contour of skull, proodont incisors and enlarged first molars. The skull of *sublimis* agrees with those of *pictus* and *boliviensis* in general characters, but is smaller than either and less angular than that of *boliviensis*. Angle of projection of inci-

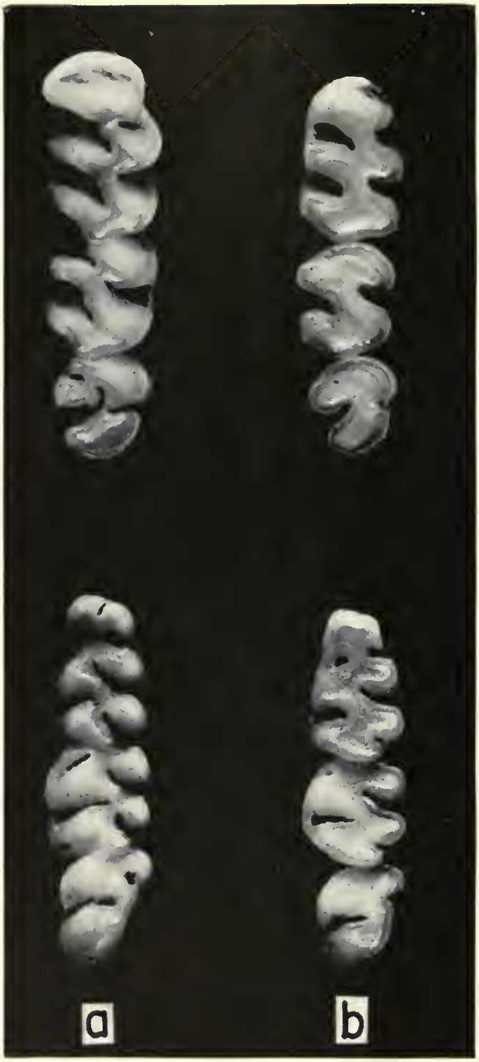


FIG. 99.—*Phyllotis sublimis.* Right upper and left lower molars of *a*, juvenal; *b*, adult.

sors, relative to long axis of skull, is intermediate in position between the more proodont incisors of *boliviensis* and the more orthodont incisors of *pictus*. Molars of *sublimis* are essentially as in *boliviensis* except for the weaker procingulum of m^2.

Variation.—Differences in size, notably of the molar row, between the mice of such nearby localities as Sumbay and Salinas in

Arequipa, Peru, are of approximately the same magnitude as those given by Pearson (1958, pp. 446, 466) for separating *leucurus* of the southern half of the specific range from *sublimis* of the northern half. Underparts appear to be whitish or gray depending on the proportional length of the whitish-tipped terminal portions of the hairs to the plumbeous basal portions. A series from the humid locality, El Cumbre, La Paz, Bolivia, on the eastern slope of the Andes, is darker than specimens from the comparatively dry altiplano of southern Peru.

Habitat and habits.—In describing *Phyllotis sublimis*, Thomas (1900, p. 468) observed that the species "lives at the highest altitude [type locality, 5500 meters] from which mammalian life has been recorded in the New World, and in the Old is only surpassed in this respect by a few of the Himalayan species."

Actually, a number of other species of rodents, carnivores and ungulates live at the same elevations as *P. sublimis*. The determining factor in these cases is not altitude *per se* but the points at or below the limits of perpetual snow where suitable food is found. Permanent snow line in Peru varies locally from under 5000 to 5800 meters above sea level.

Phyllotis sublimis is, according to Pearson (1951, p. 147), "one of the commonest mice of the altiplano of southern Peru. It is nocturnal and seems to prefer the shelter of rocks in rather open, grassy places. A stone corral in a field of ichu grass is an ideal habitat, but *sublimis* will also live in abandoned tuco-tuco diggings, in rock piles, in stunted thorn and sage . . . or among boulders or *jareta*. It shares these habitats with one or more of the following: *Phyllotis darwini* subsp. [=*rupestris*], *P. boliviensis flavidior*, *Hesperomys*, *Neotomys*, *Akodon jelskii pulcherrimus*, and *A. andinus lutescens*. Because it prefers grassy places, it is more frequently found in valleys than on barren or rocky hilltops. It seems to be gregarious, for many times I have caught several at the same place, and Thomas [supra cit.] reported that the type and 8 topotypes were all dug out of one burrow.

"The most puzzling thing about these mice is their disappearance during October, November, and December. They were found in considerable numbers at Pairumani and Santa Rosa during July, and at Caccachara in August and early September. Thirty-four were trapped at Caccachara from August 16 to September 15. No more traps were set until October 4, whereupon considerable trapping in likely terrain was carried out until early December, yet not one more *sublimis* was caught during this time. Nor were any caught at Cailloma, Pairumani, and Caccachara in December of 1939. It seems likely that either the population was greatly reduced by disease in September in 1939 and 1946 . . . or that *sublimis* remains below ground, possibly hibernating during much of October, November, December, and perhaps subsequent months. We saw no evidence of an epizootic nor of hibernation (except that one specimen was recorded as fat on July 15) but none of the later specimens were skinned and, therefore, subcutaneous fat deposits may have been overlooked. Sanborn has kindly given me additional dates of capture of *sublimis*. These also suggest a disappearance during the wet season; his latest capture was October 7 and the earliest, April 30." Pearson suggests the possibility that " 'Hibernation' during the southern hemisphere summer would not be totally unexpected in the case of *P. sublimis*, because this mouse is nocturnal. Its unusually long, soft, thick fur would be good protection in the cold dry nights of winter; but might wet easily in the warmer nights of summer when the ground is frequently covered with wet snow. Such an escape (if it occurs) from wet and snow in summer is unique, and should, of course, be considered a form of estivation."

In conformity with Pearson's observations, I have noted also that with the onslaught of a rainy season, after prolonged drought, there is a dramatic disappearance of certain species of usually nocturnal mice. This phenomenon is general throughout the tropical zone from sea level to the highest altitudes inhabited by mammals. The disappearance, or radical reduction in numbers, however, is not real. It is apparent only in trapping records. Non-breeding mice reduce their geographic radius of activity and the frequency of forays concurrently with the revival of plants and the sprouting of succulent grasses and herbs stimulated by the rains. In the midst of an abundance of familiar, desirable foods in natural situations, mice become trap shy and lose much of their susceptibility to bait. As Pearson points out, no specimens of *Phyllotis sublimis* were taken during the rainy season. Conversely, most successful trapping occurs toward the end of the dry season, when food plants are scarce and low in food value. In the case of *P. sublimis*, this period coincides with the recorded breeding season when sexually stimulated mice are extremely active, least wary, and most prone to being trapped.

Reproduction.—The following is quoted from Pearson (1951, p. 147): "Males at Pairumani in mid-July had small testes (3 mm.), whereas those at Santa Rosa at the end of July were in breeding condition (testes 7 to 8 mm.). Males at Caccachara, however, did not reach breeding condition until September 3. None of the females contained embryos through September 15, when the last capture was made. It is interesting to speculate upon the time of reproduction if they estivate at the season when the other mice are reproducing. The ratio of sexes was 30 males to 21 females." Later Pearson (1958, p. 447) observed that "young females are sexually precocious. One specimen in gray juvenile pelage and with head and body only 86 mm. long contained a vaginal plug; another specimen with head and body 89 mm. and skull 23.8 mm. long was in an early stage of pregnancy." Sexual precocity in phyllotines has already been noted in *P. darwini* and *P. osilae*.

Phyllotis sublimis sublimis Thomas

Phyllotis sublimis Thomas, 1900, Ann. Mag. Nat. Hist., (7), **6**: 467. Koford, 1954, Invest. Zool. Chilenas, **2**: 95—CHILE: *Antofagasta* (Toconce).

E[*uneomys*] *sublimis*, Thomas, 1901, Ann. Mag. Nat. Hist., (7), **8**: 254—classification.

Euneomys sublimis, Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9**: 134—BOLIVIA: *Cochabamba* (Cosmini). Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9**: 226—BOLIVIA: *Oruro* (Livichuco).

[*Euneomys* (*Auliscomys*)] *sublimis*, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 143—classification.

[*Phyllotis* (*Auliscomys*)] *sublimis*, Osgood, 1915, Field Mus. Nat. Hist., Zool. Ser., **10**: 191—classification.

Phyllotis (*Auliscomys*) *sublimis*, Sanborn, 1950, Mus. Hist. Nat. "Javier Prado," (A), Zool., no. 5: 7—PERU: *Arequipa* (Salinas; Sumbay); *Puno* (Yunguyo). Pearson, 1951, Bull. Mus. Comp. Zool., **106**: 147—PERU: *Puno* (Pairumani; Santa Rosa; Caccachara).

Phyllotis sublimis sublimis, Pearson, 1958, Univ. California Publ. Zool., **56**: 447—BOLIVIA: *La Paz; Oruro;* PERU: *Apurimac; Arequipa; Ayacucho; Puno; Tacna* (for specific localities see explanation of fig. 97, p. 421); revision.

Phyllotis (*Auliscomys*) *sublimis leucurus*, Sanborn (not Thomas) 1950, Mus. Hist. Nat. "Javier Prado," (A), Zool., no. 5: 8—BOLIVIA: *La Paz* (El Cumbre).

Phyllotis sublimis leucurus, Pearson (part, not Thomas), 1958, Univ. California Publ. Zool., **56**: 448—CHILE: *Antofagasta* (Toconce).

Hesperomys lepidus montanus, Sanborn (part, not Sanborn), 1950, Mus. Hist. Nat. "Javier Prado," (A), Zool., no. 5: 4—BOLIVIA: *La Paz* (El Cumbre, juvenals only).

Type.—Female, skin and skull, British Museum (Natural History) no. 0.10.1.60; collected 18 June, 1900, by Perry O. Simons.

Type locality.—Rinconado Malo mountain pass, above Cailloma, on road to Sumbay, Arequipa, Peru; altitude said to be 5500 meters above sea level.

Distribution (fig. 97).—Highlands of southern Peru, northeastern Chile and western Bolivia from southern Ayacucho and Apurimac through Arequipa and Puno, in Peru, into Antofagasta, Chile, and La Paz and Oruro, Bolivia; altitudinal range approximately from 3800 to 5625 meters above sea level.

Characters.—A small, pale, short-tailed, thickly furred vole-like mouse, as described for the species.

Taxonomy.—Undoubted representatives of typical *sublimis* are from the Pacific and Lake Titicaca drainage basins of southern Peru. Specimens from El Cumbre, Bolivia, referred to *Phyllotis sublimis leucurus* and *Hesperomys lepidus montanus* by Sanborn, are from the head of the Río La Paz in Amazonian drainage. They are darker throughout than true *sublimis*. Pearson (1958, pp. 447–448) also treats them as inseparable from typical *sublimis*. On the other hand he notes that "three unusually short-tailed specimens from the Province of Antofagasta, northern Chile, are somewhat paler than typical *sublimis sublimis* and have relatively large tooth rows but white bellies" and he refers them to *leucurus*. Pearson's measurements for the Toconce specimens are reproduced in Table 57. If, as Pearson affirms, the only significant differences between *sublimis* and *leucurus* are in the length of the molar row and color of the belly, the Toconce series is certainly indistinguishable from typical *sublimis*.

Measurements.—See Table 57.

Specimens examined.—33. PERU.—*Arequipa:* Salinas, 6 (CNHM); Sumbay, 6 (CNHM). *Puno:* Huacullani, 5 (CNHM); San Antonio de Esquilache, 3 (CNHM); Yunguyo, 6 mi. south, 1 (CNHM); Santa Lucía, 1 (CNHM). BOLIVIA.—*La Paz:* El Cumbre, 11 (AMNH).

Phyllotis sublimis leucurus Thomas

Euneomys (*Auliscomys*) *leucurus* Thomas, 1919, Ann. Mag. Nat. Hist., (9), **4**: 129, footnote. Thomas, 1921, op. cit., (9), **8**: 612—ARGENTINA: *Jujuy* (Sierra de Zenta; La Lagunita).

[?]*Auliscomys leucurus*, Thomas, 1926, Ann. Mag. Nat. Hist., (9), **18**: 194—BOLIVIA: *Potosí* (Lipez).

Phyllotis (*Auliscomys*) *sublimis leucurus*, Sanborn, 1950, Mus. Hist. Nat. "Javier Prado," (A), Zool., no. 5: 8—part, classification.

Phyllotis sublimis leucurus, Pearson, 1958, Univ. California Publ. Zool., **56**: 448—part, ARGENTINA: *Jujuy* (La Lagunita; Sierra de Zenta); BOLIVIA: *Potosí* (Lipez).

Type.—Adult female, body in alcohol, skull separate, British Museum (Natural History) no. 19.7.10.3.

Table 57. Measurements of the subspecies of *Phyllotis sublimis* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
PERU							
sublimis							
Rinconado[1]	105	54	23(s.u.)	23	25.3	14.5	4.7
Salinas	117(108–125)5	55(52–62)5	23(21–25)5	21.5(21–22)3	28.2(27.9–28.7)4	15.4,16.1	5.5(5.2–5.8)5
Sumbay	96,97,100,109	46,43,55,61	22,22,22,23	21,20,—,23	25.5,24.9,25.5,—	14.4,14.0,14.6,—	5.2,5.1,5.1,5.2
Huacullani	98,104,113	54,54,54	21,23,23	—,—,—	26.3,26.2,27.2	14.7,15.2,15.4	5.0,5.0,4.7
San Antonio	108,113,114	47,52,51	22,22,21	—,—,—	26.5,27.4,27.6	15.1,15.4,16.2	4.9,5.2,5.3
BOLIVIA							
El Cumbre	111(99–121)11	55(48–59)11	22(21–23)11	—	28.1(27.2–29.1)10	15.4(14.6–16.1)10	5.0(4.6–5.3)11
CHILE							
Toconce[2]	109(107–111)3	46(45–48)3	23,23,23	22.3(20–24)	27.8(27.7–28.0)2	15.3(15.1–15.5)3	5.3(5.3–5.4)3
leucurus							
La Lagunita[3]	102	58	21.3	20	30.5	16.3	5.7

[1] Type of *sublimis*, from original description.

[2] *Ex* Pearson (1958, p. 466).

[3] Type of *leucurus* (in spirits), from original description.

Type locality.—La Lagunita, east of Maimará, Sierra de Zenta, Jujuy, Argentina; altitude, 4500 meters above sea level.

Distribution (fig. 97).—High Andes of Jujuy, northern Argentina and Potosí, southwestern Bolivia; altitudinal range between 4500–4700 meters above sea level.

Characters.—Originally said to differ from typical *sublimis* "by the greater size of its skull;" according to Pearson (1958, p. 447) "specimens from southern Bolivia and northern Argentina have longer tooth rows and grayer bellies but otherwise agree well with typical *sublimis.*"

Remarks.—External measurements of the type were taken from the shrunken specimen preserved in spirits. Cranial dimensions, however, indicate an adult, probably very old, and larger than any of the available specimens of *P. sublimis sublimis.* Besides the type, Thomas recorded 4 paratypes, 5 specimens from Sierra de Zenta, and 8 from Lipez, without data. Most of these were examined by Pearson (1958, p. 448) and found to be "gray bellied and [with] large teeth, hence . . . placed with *leucurus.*"

As noted under the species heading, differences in molar row length and color of underparts between northern and southern populations of the species are not significantly greater than differences between local populations in Arequipa Department, Peru. Pearson (1958, p. 448) lists 13 specimens from southern Bolivia (Lipez, 8) and northern Argentina (La Lagunita, 2, and Sierra de Zenta, Jujuy, 3) but lumps measurements for only 5 from "Lipez (Bolivia) and Province of Jujuy."

Measurements.—See Table 57.

Specimens examined.—None.

Phyllotis gerbillus Thomas

Phyllotis gerbillus Thomas, 1900, Ann. Mag. Nat. Hist., (7), **5**: 151—PERU: *Piura* (Piura; Catacoas). Thomas, 1900, op. cit., p. 356—comparison.

Paralomys gerbillus, Thomas, 1926, Ann. Mag. Nat. Hist., (9), **17**: 315—generic type.

Type.—Adult female, skin and skull, British Museum (Natural History) no. 0.1.1.30; collected 12 April, 1899, by Perry O. Simons.

Type locality.—Piura, Piura, northwestern Peru; altitude 50 meters above sea level.

Distribution (figs. 57, 100).—Known only from the neighborhood of Piura and nearby Catacoas, both localities in the Sechura

Desert, Piura, northwestern Peru. The range of *Phyllotis gerbillus* is less than that of any other phyllotine and is one of the most restricted of South American mammals. No other cricetine has been recorded from the same area.

External characters.—Smallest member of the *Phyllotis* section, and smaller than most *Calomys;* coloration gerbil-like; tail subequal to combined head and body length, thinly haired white throughout, sometimes with an occasional dark hair or patch of hairs; integument of terminal one-fourth or one-third of tail dark brown, contrasting sharply with whitish basal portion, pencil rudimentary; hind foot (fig. 3) broad and short (19–21 mm.), sole sparsely set with whitish bristles except on six well-developed pads; ear comparatively small, its length measured from notch, appreciably less than that of hind foot, a white preauricular tuft usually present; upper parts of head and body ochraceous or salmon-color finely peppered with dark brown; upper half of sides of body like back but hairs without dark tipping, lower half wholly white like underparts; hairs of limbs, cheeks, sides of rostrum white to roots.

Cranial characters (fig. 101).—Sides of supraorbital region divergent, the edges square, without beading or ledges; zygomatic arches more or less parallel-sided, greatest breadth between them less than distance from posterior tips of nasals to anterior border of supraoccipital; braincase not inflated; interparietal well developed; bulla moderately large, its antero-posterior length, less tube, equal to or more than, length of molar row; outer side of mandible with capsular projection encasing base of incisor.

Dental characters (figs. 101, 102).—Incisors ungrooved, opisthodont; molar rows parallel-sided; upper and lower first molars 4-rooted; molar crowns low, slightly terraced; second and third molars with tendency to involute or laminate, a sigmoid or figure 8 crown pattern resulting; upper cusps ovate, lower subtriangular; procingulum of m^2 moderately developed, the first primary fold well defined and persistent; minor fold of m_2 present.

Comparisons.—The bright sandy-colored upper parts of head and body of *Phyllotis gerbillus* contrasting sharply with the white of lower half of sides, limbs, cheeks and white-haired tail is strikingly similar to the color pattern of northern Argentine representatives of *Eligmodontia typus.* The first is readily distinguished from the other by its narrower, less hairy feet with the three postdigital plantar pads not coalesced to form a hairy cushion. The short-tailed, comparatively small-eared North American *Peromyscus polionatus* is also similarly colored, but is too distantly related to require more than incidental mention. Nearest geographic, as well as phyletic ally is the slightly larger, allopatric *Phyllotis amicus,* with comparatively dark upper parts, sides of body and limbs, much larger ears and longer, sharply bicolor, more hairy tail. Cranially and dentally, *gerbillus* retains the more primitive features of less expanded braincase, smaller auditory bullae and less planed molars. However, the greater tendency for lamination in the molars of *gerbillus* as compared with those of *amicus,* is an advanced condition.

Variation.—All known specimens of *Phyllotis gerbillus* are from the region about Piura. Individual variation, the only kind of variation, except possibly crop variation, that can occur here, is remarkably slight. In some specimens the dorsal surface is nearly uniformly ochraceous, in others the dorsum is sandy in appearance because of the greater amount of dark brown tipping to the cover hairs. These two conditions are equivalent to the fully intergrading pale and dark color phases of normal occurrence in mice. In one juvenal hair bases of outer sides of thighs are plumbeous, in all others the hairs are wholly white.

Habits and habitat.—The notation on the original label of a topotype collected by Perry O. Simons is "in pile of brush." Nothing more is known regarding the habits of the Piura desert mouse. Seventeen specimens of *Phyllotis gerbillus* collected by Celestino Kalinowski, 5 kilometers east of Piura, were secured in 1954 during the course of three trap nights (July 11, 18, 19). No other mammal was taken in the locality and no other cricetine rodent has ever been recorded from the Piura coast.

Remarks.—The striking coloration of *Phyllotis gerbillus* Thomas, its desert habitat and uncertainty regarding its exact generic position induced Thomas (1926a, p. 315) to regard the mouse as representing a new genus he named *Paralomys.* It was said to be nearest related to *Eligmodontia.* Ellerman (1941, pp. 446, 448) referred *Paralomys* to *Hesperomys* (=*Calomys*) but his definition of *Hesperomys* excludes it. Osgood (1947, p. 171) restored the Peruvian desert mouse to *Phyllotis* but as a subgenus. He observed, however, that "no very unusual generic or subgeneric characters for it [*Paralomys*] have been pointed out."

Measurements.—See Table 58.

Specimens examined.—23. PERU.—*Piura:* Piura, 6 (CNHM, 1; USNM, 5); 5 kilometers east of Piura, 17 (CNHM).

TABLE 58.—Measurements of *Phyllotis gerbillus* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
Piura[1]	82	90	20[2]	17	24.0	12.3	3.5[3]
Piura	75	76	21[2]	17	23.2	12.2	3.7
Piura, 5 km. E.	80(72–93)13	79(72–97)13	20(19–21)13	17.6(17–18)13	23.1(22.0–24.2)10	12.2(11.7–13.1)10	3.8(3.6–4.0)10

[1] Type, from original description.

[2] Without claw.

[3] Crown length.

EXPLANATION OF FIGURE 100

Phyllotis gerbillus and *P. amicus:* collecting localities and collectors.

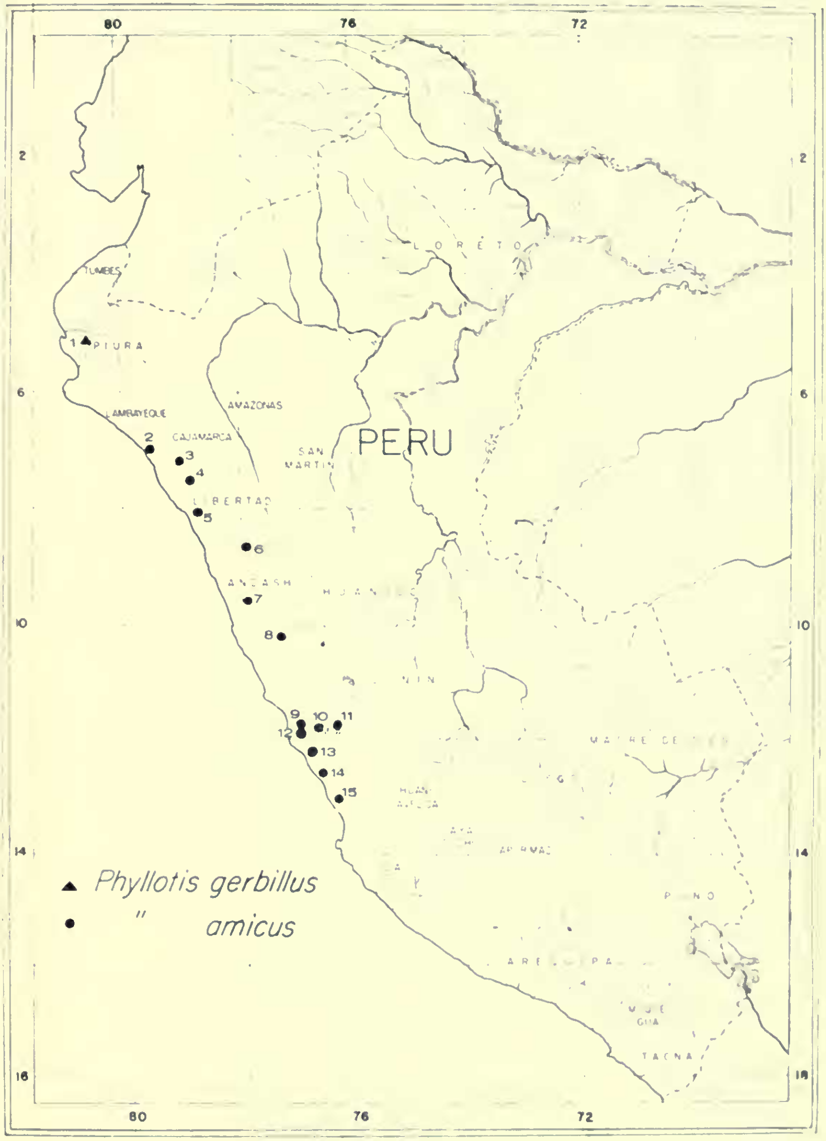
Type localities in **boldface.**

Phyllotis gerbillus (1)

1. **Piura, Piura.**—P. O. Simons; C. Kalinowski.

Phyllotis amicus (2–15)

2. **Etén, Lambayeque.**—Type locality of *maritimus;* P. O. Simons at 10–15 meters.
2. Reque, Lambayeque. —P. O. Simons.
3. **Tolón, Cajamarca.**—Type locality of *amicus;* P. O. Simons at 100 meters.
4. Tambo, Río Shigray, Cajamarca.
5. Menocucho, Libertad. —W. H. Osgood and M. P. Anderson.
6. **Uramarca** [=Yuracmarca], **Ancash.**—Type locality of *montanus;* P. O. Simons at 1200 meters.
7. Pariacoto, Huaraz, Ancash. —C. Kalinowski at 1360 meters.
8. Marca, Ancash.
9. Chocas, Lima, 2000 feet.
10. Chosica, Lima. —C. C. Sanborn at 3000 feet.
11. Puente Carrión, Lima. —M. Puestas at 1700 meters.
12. Loma Viscacheras, Lima. —E. Zuñiga at 1000 meters.
13. La Palma, Lima, 200 feet.
14. San Antonio, Lima, 50 feet.
15. Cañete, Lima, 100 feet.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72
2
6
10
14
18
TUMBES
PIURA
LAMBAYEQUE
CAJAMARCA
AMAZONAS
SAN MARTIN
LORETO
PERU
LIBERTAD
ANCASH
HUANUCO
JUNIN
MADRE DE DIOS
HUANCAVELICA
AYACUCHO
APURIMAC
PUNO
AREQUIPA
MOQUEGUA
TACNA
1
2
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4
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7
8
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10
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15
▲ Phyllotis gerbillus
● " amicus

FIG. 100.—Collecting localities of *Phyllotis gerbillus* and *P. amicus*. See opposite page for explanation.

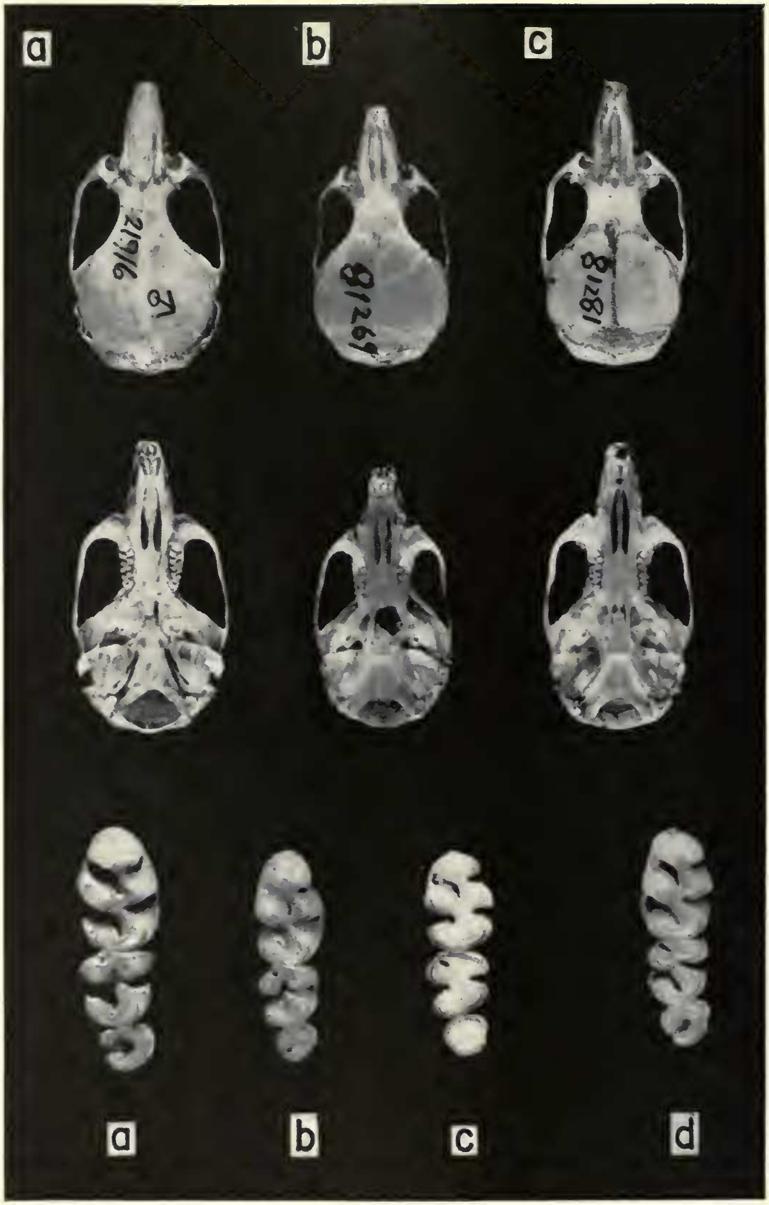
a
b
c
21916
81269
81281
a
b
c
d

FIG. 101.—*Phyllotis gerbillus* and *P. amicus*. *a–c*, dorsal and ventral aspects of skulls and right upper molars of *P. gerbillus; d*, right upper molars of *P. amicus*. (Skulls slightly more than × 1½.)

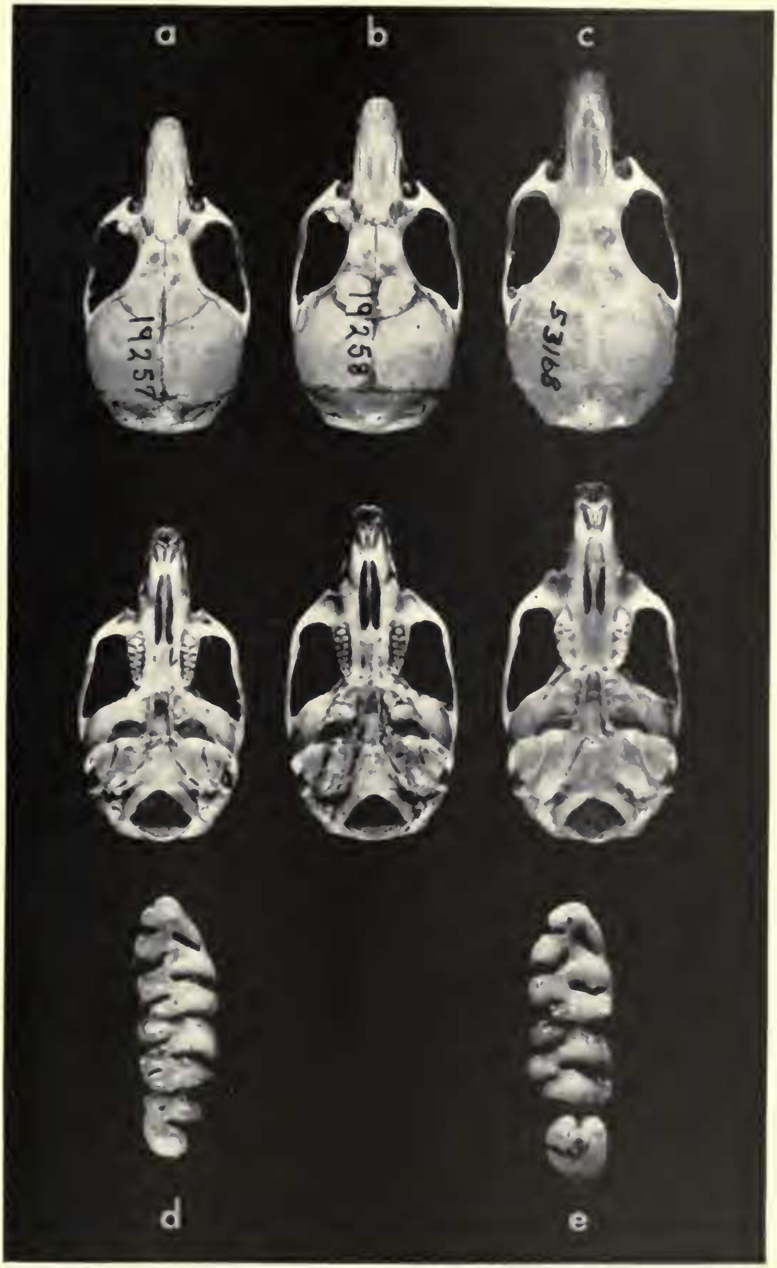
a
b
c
19257
19258
53168
d
e

FIG. 102.—*Phyllotis amicus* and *P. gerbillus*. *a–c*, dorsal and ventral aspects of skulls of *P. amicus; d*, right lower molars of *P. amicus; e*, right lower molars of *P. gerbillus*. (Skulls slightly less than × 2.)

Phyllotis amicus Thomas

Phyllotis amicus Thomas, 1900, Ann. Mag. Nat. Hist., (7), **5:** 355—*Lambayeque* (Etén; Reque). Thomas, 1900, op. cit., (7), **6:** 296–297—*Cajamarca* (Tolón); *Lima* (Chosica). Osgood, 1914, Field Mus. Nat. Hist., Zool. Ser., **10:** 166—*La Libertad* (Menocucho). Osgood, 1916, op. cit., **10:** 207—comparisons.

Phyllotis amicus amicus, Pearson, 1958, Univ. California Publ. Zool., **56:** 445—*Cajamarca* (Tolón); *La Libertad* (Menocucho); Lima (Barfa Blanca[?]; Cañete; Chocas; Chosica; La Palma; Loma Viscacheras; Mamgomarca[?]; Puente Carrión; San Antonio; Santa Eulalia; Surco).

Phyllotis amicus maritimus Thomas, 1900, Ann. Mag. Nat. Hist., (7), **6:** 296—*Lambayeque* (type locality, Etén). Pearson, 1958, Univ. California Publ. Zool., **56:** 445—*Lambayeque* (Etén; Reque).

Phyllotis amicus montanus Thomas, 1900, Ann. Mag. Nat. Hist., (7), **6:** 296, 297—*Ancash* (type locality, Uramarca, Río Ushpe, near Pallasca, 1200 meters altitude; Marca, 2000 meters altitude); *Cajamarca* (Tambo, Río Shigray Pearson, 1958, Univ. California Publ. Zool., **56:** 445—*Ancash* (Huallanca; Marca; Pariacoto; Shigray Tambo; Uramarca); *La Libertad* (Otusco).

Type.—Male, British Museum (Natural History) no. 0.3.1.94; collected 2 November, 1899, by Perry O. Simons.

Type locality.—Tolón, Cajamarca, Peru; altitude, 100 meters above sea level.

Distribution (figs. 57, 100).—Western Peru, on the Pacific slope of the Cordillera Occidental from the department of Lambayeque south into southern Lima; altitudinal range, sea level to about 2000 meters above.

External characters.—Average size less than that of other species of *Phyllotis* except *P. gerbillus;* tail always longer than combined head and body length, brown above, gray or buffy beneath, terminal portion moderately bushy, the tip with a short but well defined pencil; hind foot well developed (21–24 mm.) with a few minute hairs on plantar surface; ear large, nearly or quite as long, measured from notch, as hind foot with claw; postauricular patch not evident. Upper parts buffy, ochraceous or tawny with a fine mixture of black or dark brown; sides of body and limbs with less black, usually defined from underparts by an ochraceous lateral line; underparts, inner sides of limbs and cheeks whitish or gray with or without a pale, buffy wash, the individual hairs slaty basally.

Cranial characters (figs. 58, 102).—Skull generally as in *P. gerbillus,* but braincase more inflated than in other species of *Phyllotis;* sides of supraorbital region divergent from angle behind fronto-maxillary region; greatest width of rostrum less than interorbital breadth at midfrontal plane; zygomatic arches not markedly expanded; interparietal fully developed; auditory bulla well inflated, its anteroposterior length, less tube, more than alveolar length of molar row; outer side of mandible with capsular projection encasing base of incisor.

Dental characters (figs. 49, 67, 101,*d*, 102,*a–d*).—Incisors short, opisthodont, ungrooved; molar rows parallel-sided or slightly convergent posteriorly; upper first molars 4-rooted, lower 3- or 4-rooted; molar crowns low, plane or slightly terraced; outline of upper cusps ovate, of lower subtriangular, unworn second upper molars involuted, not tending to laminate as in *gerbillus;* moderately worn crown with a modified sigmoid pattern that becomes 8-shaped with increased wear; procingulum of m^2 moderately developed, the first primary fold well defined and persistent in moderately worn tooth; minor fold of m_2 present.

Comparisons.—Comparisons with *Phyllotis gerbillus* have been made in connection with the description of that species (p. 432) and are implicit in the above characterization of *P. amicus*. *P. amicus* is distinguished from sympatric representatives of *P. andium* by smaller average size, proportionately longer and more hairy tail, ear larger and nearly or quite as long as hind foot, skull with broad divergent-sided supraorbital region always wider mid-frontally than greatest width of rostrum; incisors more delicate; procingulum of m^2 with first primary fold more developed and persistent except in extremely worn tooth.

Taxonomy.—Three races of *Phyllotis amicus* were described by Thomas. From the desert coast, he distinguished a pale form (*maritimus*). The typical race (*amicus*) was described from farther inland at slightly higher elevations. It was said to be larger and darker than *maritimus*. From 1200 meters on the Andean coastal range Thomas discerned a still larger form (*montanus*) described as paler than *amicus* and with longer tail and larger ears. Material at hand confirms the overall increase in size from the coast eastward into the Andes. It also appears that populations of the dry coastal plain are paler than those of the coastal lomas and that the latter, in turn, are darker than Andean populations living at altitudes above 100 meters. The differences, however, are slight, fully intergrading and contained within such narrow geographic limits that retention of nominal distinctions between the populations does not appear to be justified.

Additional data presented by Pearson (1958, pp. 443–445) since the above was written prove that the differences between the three

TABLE 59.—Measurements of *Phyllotis amicus* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of upper molar row
PERU							
Tolon[1]	82	105	23	23	24.4	12.7	3.8
Tolon[2]	85.2	100	22.6	22.6	—	—	—
Eten[3]	80	100	22	22.5	—	—	—
Eten[4]	78.5	96.6	—	22.25	—	—	—
Uramarca[5]	93	122	24	26	—	—	—
Uramarca[6]	90	117.5	24	24.75	—	—	—
Tambo[7]	90	111	22.75	24.75	—	—	—
Chosica[8]	85	107.5	23	22.5	—	—	—
Chosica	92(86–100)4	106(103–111)3	22.5(22–23)4[9]	21.4(20–23)4[10]	25.8(25.1–26.9)3	12.9(12.7–13.2)4	3.9(3.8–4.0)4
Menocucho	85(78–96)7	106(100–112)7	21.5(20–22.5)7[9]	20.3(19–21.5)7[10]	24.1(23.4–25.0)6	11.8(11.4–12.0)7	3.7(3.5–3.9)7
Viscacheras	100(?)	100(?)	21.5[9]	21[10]	26.2	—	4.3
Carrión	—	—	22[9]	22[10]	26.3	13.0	4.0
Pariacoto	101(97–109)5	113(108–116)5	22.5(21.5–23)5[9]	22.1(21.5–22.5)5[10]	26.3(25.5–27.8)4	13.3(12.6–13.8)5	4.3(4.1–4.4)5

[1] Type of *amicus*, from original description.

[2] Average of 5 topotypes of *amicus*, from Thomas (1900, p. 297).

[3] Type of *maritimus*, from original description.

[4] Average of 6 topotypes of *maritimus*, from original description.

[5] Type of *montanus*, from original description.

[6] Average of 4 paratypes of *montanus*, from original description.

[7] Average of 4 specimens of *montanus*, from original description.

[8] Average of 2 specimens of *amicus*, from Thomas (1900, p. 297).

[9] Dry, from heel to longest claw.

[10] Dry, from notch, without compensation for shrinkage.

nominal races are even less than specimens in the collection of Chicago Natural History Museum led me to believe. Pearson reasoned, however, that inasmuch as *amicus*, with the prior name, was intermediate and poorly defined from the other two, all three nominal subspecies should be recognized.

Habits and habitat.—Nothing is known of the life history of *Phyllotis amicus*. Its morphological characters and geographic distribution suggest a dominantly seed-eating inhabitant of sand and rock formations with sparse cover.

Measurements.—See Table 59.

Specimens examined.—20. *Lima:* Chosica, 4 (CNHM); Loma Viscacheras, 1 (CNHM); Puente Carrión, 1 (CNHM); *La Libertad:* Menocucho, 7 (CNHM); *Ancash:* Pariacoto, Huaraz, 5 (CNHM); *Cajamarca:* Tolón, 2 (USNM).

Phyllotis griseoflavus Waterhouse. (Synonymy under subspecies.)

Distribution (figs. 57, 103).—Argentina, Paraguay, and Bolivia and, possibly, Mato Grosso, Brazil, from sea level to about 3000 meters above.

EXPLANATION OF FIGURE 103

Phyllotis griseoflavus: collecting localities and collectors.
Type localities in **boldface.**

Phyllotis griseoflavus domorum (1–8)

BOLIVIA
1. Parotani, Cochabamba.—R. H. Becker, L. E. Miller, and H. S. Boyle.
2. Tapacari, Cochabamba.—P. O. Simons at 3000 meters.
3. Tin Tin, Cochabamba.—F. B. Steinbach.
4. Aiquile, Cochabamba.—F. B. Steinbach.
5. Comarapa, Santa Cruz.—F. B. Steinbach.
6. Florida, Santa Cruz.—W. Delgadillo.
7. Sucre, Sucre, 2915 meters.—P. O. Simons at 2700–3000 meters.
8. El Cabrado, Potosí.—P. O. Simons at 3500 meters.

Phyllotis griseoflavus griseoflavus (9–15)

BOLIVIA (9–11)

9. Guanacos, Santa Cruz.—F. B. Steinbach at 700 meters.
10. Tablada, Tarija.—E. Budín.
11. Tupiza, Potosí.—E. Budín at 2000 meters.

PARAGUAY (12–18)

12. Guachalla, Chaco.—P. Willim.
13. Colonia Fernheim, Chaco.—P. Willim.

Explanation of Figure 103 (*continued*)

14. Puerto Casado, Chaco.—P. Willim.
15. Makthlawaiya, Chaco.—E. Kaempfer at 400 feet.
16. Jesematathla, Chaco.—Not precisely located; Marquis de Wavrin.
17. Waikthlatingwayalwa, Chaco.—G. Kerr.
18. San Francisco Mission, Río Pilcomayo, Chaco.—Not precisely located; Borelli.

ARGENTINA (19–44)

19. Manuel Elordi, Río Bermejo, Salta.—E. Budín at 500 meters.
20. El Desmonte, Metán, Salta.—E. Budín at 500 meters.
20. Macapillo, Metán, Salta.—E. Budín at 500 meters.
20. La Represa, Metán, Salta.—E. Budín at 500 meters.
21. Río Cachi, Salta.—C. Spegazzini.
22. Villa Carolina, Jujuy.—E. Budín at 500 meters.
23. Tapia, Tucumán.—E. Budín at 500 meters.
24. Belén, Catamarca.—E. Budín at 800 meters.
24. Corral Quemado, Belén, Catamarca.—E. S. Riggs.
25. Puntilla, Tinogasta, Catamarca.—E. Budín at 1000 meters.
25. Tinogasta, Catamarca.—E. Budín.
26. Otro Cerro, "Rioja"=Catamarca.—E. Budín at 3000 meters.
27. Chumbicha, Catamarca.—E. Budín at 600 meters.
28. Lavalle, Santiago del Estero (463 meters).—L. E. Miller and H. S. Boyle at 1800 feet.
29. Tacañitas, Santiago del Estero.—J. Yepes.
30. Avia Terai, Chaco.—L. E. Miller and H. S. Boyle at 450 feet.
31. Las Palmas, Chaco.—Názara and Amigo.
32. Cruz del Eje, Córdoba (457 meters).—P. O. Simons at 600 meters.
33. La Paz, Córdoba (681 meters).—J. Yepes.
34. General Roca, La Rioja.—M. P. Gomez.
35. Potrerillos, Cordillera de Famatina, La Rioja.—E. Budín at 1600 meters.
36. Media Agua, San Juán.—L. E. Miller and H. S. Boyle at 2200 feet.
37. Villasuso, La Pampa.—de la Barrera.
38. Pichi Mahuida, La Pampa.—E. Budín at 650 meters.
39. Algarrobo, Buenos Aires (47 meters).—J. Yepes.
40. Chimpay, Río Negro.—C. C. Sanborn.
41. Choele-Choel, Río Negro.—E. Budín at 200 meters.
42. Río Negro (near mouth), Río Negro.—C. Darwin.
43. Rawson, Chubut.—E. Budín.
44. Port Desire (=Puerto Deseado), Comodoro Rivadavia.

BRAZIL

45. Ivinheima (Río), Mato Grosso.—F. Kühlhorn.

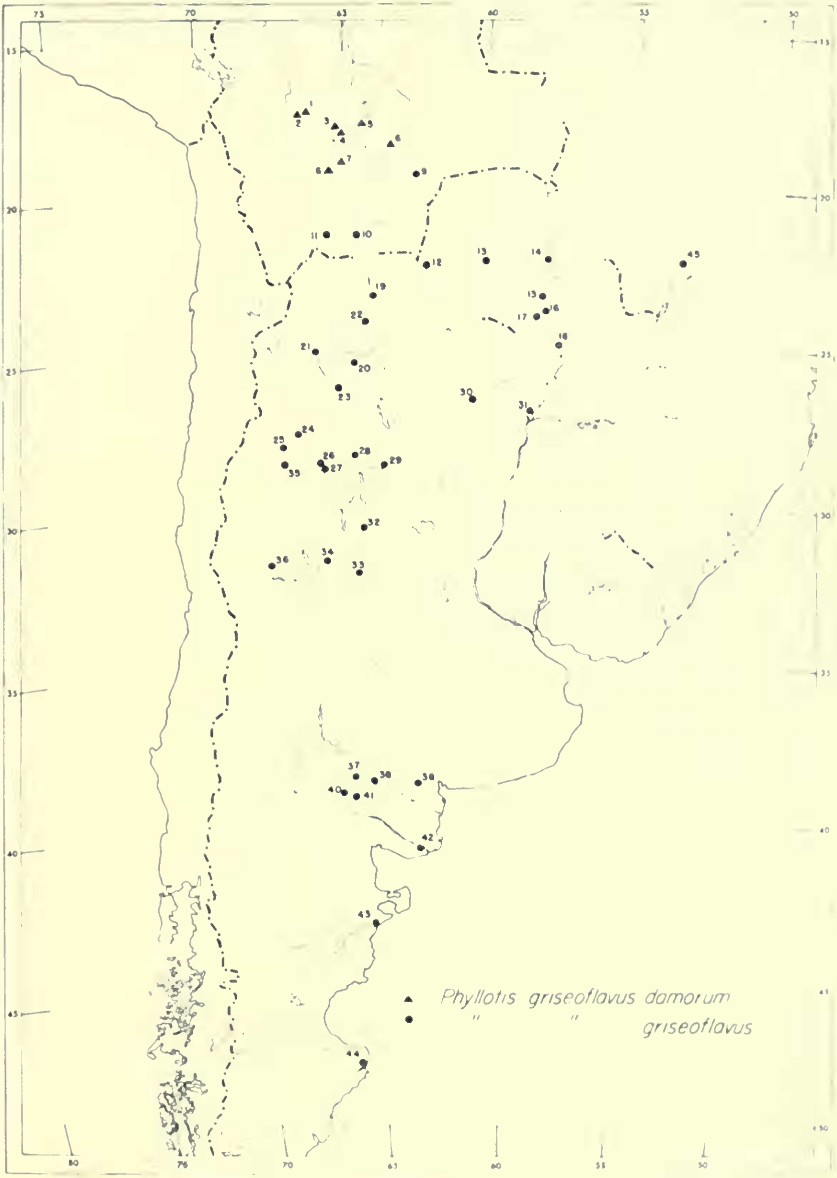
▲ Phyllotis griseoflavus domorum
● " " griseoflavus
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FIG. 103. Collecting localities of the subspecies of *Phyllotis griseoflavus*. See preceding pages for explanation.

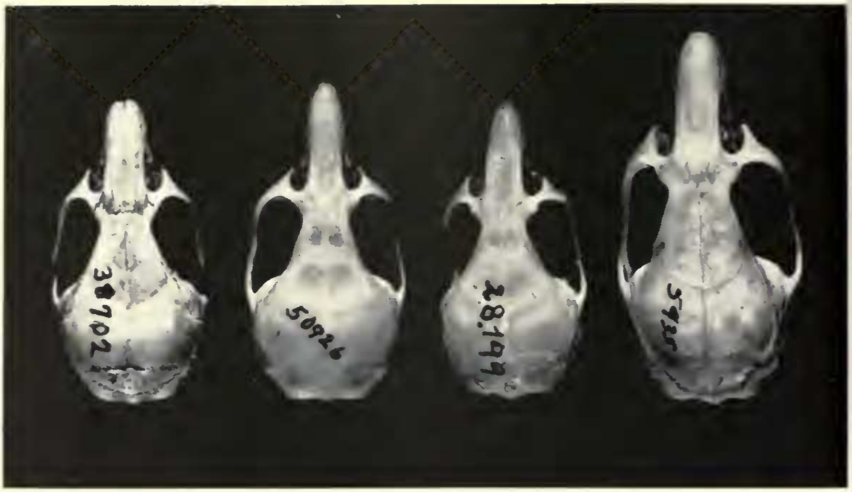

FIG. 104.—*Phyllotis griseoflavus.* Dorsal aspect of skulls, showing variation in size (about × 1⅓).

External characters.—Largest species of the genus; tail bicolor, always longer than combined head and body length, well haired with terminal portion usually bushy, tip pencilled; hind feet comparatively well developed, soles naked, plantar tubercles normal; small whitish postauricular patches sometimes present; upper parts buffy to tawny more or less mixed with gray or black; sides of body and head with less black, an ochraceous lateral line present or absent; underparts sharply defined white, hairs of chin, throat, neck wholly white, of chest and belly wholly white or slaty basally.

Cranial characters (figs. 34, 58–60, 104, 105).—Sides of broad supraorbital region of skull divergent, the edges beaded and projected laterally as ledges; zygomata usually parallel-sided, sometimes convergent anteriorly, widest distance between them less than length from posterior tips of nasals to anterior border of supraoccipital; anterior border of zygomatic plate concave, the upper corner pointed, sometimes projected as a short spinous process; incisive foramina narrow, nearly parallel-sided for most of their length; posterolateral palatal pits large; width of mesopterygoid fossa measured at base of hamular processes less than length of m^1 and less than width of parapterygoid fossa measured at same plane; parapterygoid fossa shallow; bullae well inflated, their length, less tubes, from slightly less to more than length of molar row; outer side of mandible with moderately developed capsular projection enclosing base of incisor;

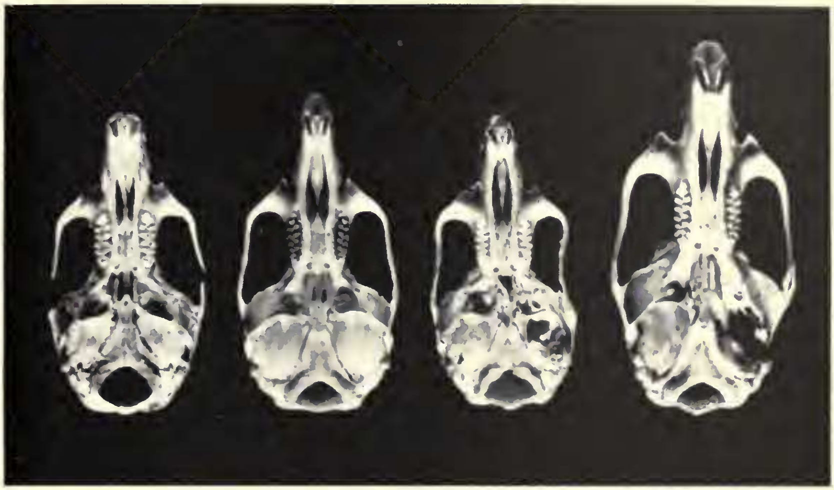

FIG. 105.—*Phyllotis griseoflavus.* Palatal aspect of skulls illustrated in fig. 104, showing variation in size.

coronoid process weak, its length from inner angle less than one-half length of condylar process.

Dental characters (figs. 67,*b*, 106, 114,*a*, 115,*f*, 116,*f*).—Incisors ungrooved, opisthodont, well developed but not heavy; molar rows parallel-sided, first upper and lower molars four-rooted; the molars slightly hypsodont, cusps plane or slightly raised but not clearly crested or terraced, triangulate, crowns of upper molars tending to lamination, crowns of lower molars less laminate, the cusps more triangulate; crown of moderately worn m^2 with a modified sigmoid pattern; anteroloph of m^2 well developed, the first primary fold distinct and persistent; posterolophid of m_2 present, the second primary fold well developed; vestigial mesoloph rarely present.

Comparisons.—The combination of large size, tail longer than combined head and body length, sharply defined white underparts, broad supraorbital region with beaded and projecting ledges distinguish *P. griseoflavus* from all other phyllotine rodents. The mesopterygoid fossa, as compared with the parapterygoid fossa, is extremely wide for *Phyllotis* and approaches the proportions of *Zygodontomys* (fig. 34), where the fossa is as wide as, or wider than, the parapterygoid fossa, measured at the same plane, and wider than length of m^1. Beaded, ledge-like supraorbital edges are also consistently present in *Zygodontomys, Calomys callosus* and usually in *Phyllotis darwini wolffsohni.* Tendency to lamination in the molar crowns of *P. griseo-*

flavus appears to result from triangulation of the cusps, a process more advanced in this than in any other species of *Phyllotis*.

The few important diagnostic differences between *P. griseoflavus* and the smaller *P. amicus* seem to confirm a suggestion made by Osgood (1947, p. 170) that the former is derived from the latter. Closer inspection of other characters leads to the conclusion, however, that both species are recent offshoots of a common but extinct ancestor. The plane, slightly hypsodont molar crowns and triangulate cusps of *P. griseoflavus* can be derived directly from the slightly terraced crowns and more ovate cusps of *P. amicus*. The form of the skull in each species is similar, but the beaded supraorbitals of *P. griseoflavus* are a specialization of the condition in *P. amicus*. On the other hand, the meso-parapterygoid fossae relationship appears to be more highly specialized in *P. amicus*. The long hairy tail is similar in both species, but the hind foot reveals some slight but highly significant differences. Except for the normal plantar tubercles, the sole of *P. amicus* is smooth or slightly granular, but that of *P. griseoflavus* retains more of the primitive scutulation and is never smooth. The ears of *P. amicus* are more enlarged than in any other species of the genus, and on the basis of this character alone, *P. griseoflavus* cannot be derived from *P. amicus*.

Variation.—Upper parts of juvenals and subadults are mouse-like in color; with maturity and increasing age they become more tawny, more heavily lined with black. Degree of hairiness of tail varies individually and, presumably, seasonally. Underparts are always sharply defined white, but basal portions of hairs vary from white to gray and deep plumbeous. Dark-based hairs are more common among juvenals and subadults than among adults, and there is a higher incidence of such hairs at the northern and southern extremes of the geographic range of the species. Hairs of ventral surface are dark at their base in 13 of 15 specimens from Río Negro and in the single Chubut specimen at hand. They are similarly dark in all 43 Bolivian highland specimens examined. Pure white hairs, or hairs with pale gray bases, predominate in central and northern Argentina, Paraguay, and in the Bolivian Chaco. Though color of base of hairs is a variable character, it acquires importance in combination with other characters. The distinction of the highland *P. g. domorum* is enhanced by the fact that all specimens referred to it on size of bullae are also provided with dark-based hairs on ventral surface. No comparable combination of characters exists for distinguishing other populations of the southern Argentine

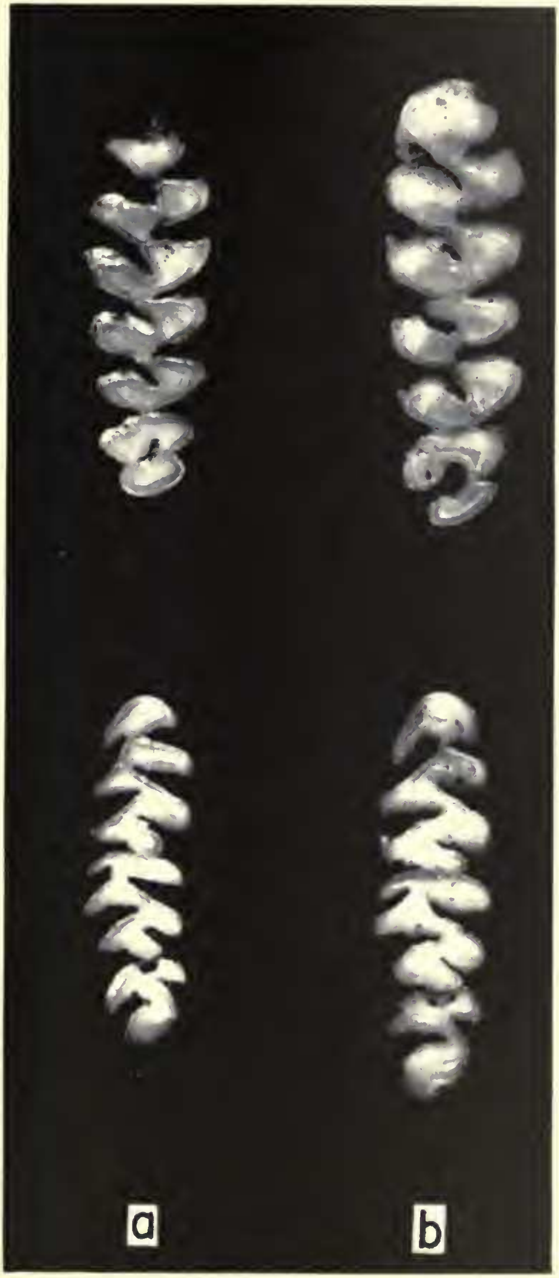

FIG. 106.—*Phyllotis griseoflavus.* Right upper and left lower molars of adults *a*, CNHM 50926 and *b*, CNHM 54357, of specimens shown in figs. 104 and 105.

species from typical *griseoflavus*. Measurements of adults reveal no appreciable geographic variation in size.

Taxonomy.—Graomys Thomas was first proposed as a genus to contain "species" *chacoensis, cachinus, domorum* and *griseoflavus*, the type. All these now prove to be conspecific. Osgood (1916, p. 207) treated *Graomys* as a subgenus of *Phyllotis*. *P. amicus* was added as a "peripheral member" that enforced the link between typical *Phyllotis* and *Graomys*. Thomas returned to the matter (1919c, p. 494) and restored *Graomys* to generic rank on the basis of "advisability." In his final classification of the rodents of the group, Osgood (1947, p. 170) insisted that *Graomys* is "a relatively recent offshoot of *Phyllotis* with connecting species still existing. Its departure from the generalized types is less than in any of the other subgenera here recognized and consistency requires that it be ranked as a subgenus rather than a genus." Osgood then distinguished two groups of large *Graomys*. The first, with four named forms, was characterized by "large audital bullae and mainly pure white underparts (in adults);" the second, marked by "smaller bullae and underparts largely with dark-based hairs," was represented by three named forms.

From the foregoing, it is evident that the primary motive for erection and retention of *Graomys* as a supraspecific taxon was the belief that it was polytypic. Putting aside species *edithae* Thomas and *hypogaeus* Cabrera[1] of uncertain affinities and not parts of the original *Graomys*, the members of the proposed genus resolve themselves into the single species and genotype, *Phyllotis griseoflavus*. There is no good reason for treating this species as anything more within the genus *Phyllotis*.

Habits and habitat.—Phyllotis griseoflavus is scansorial and adapts itself to most terrestrial and arboreal habitats. Collectors' notes on labels of specimens reveal that the animal has been found on stream embankments, among rocks, along fences, in hollow logs, wood piles and brush heaps. The original series of 13 specimens of *P. g. domorum* Thomas was taken in a house.

The following observations on the species in Chubut, Argentina, were made by Henry Durnford (*in* Thomas, 1898a, p. 210): "This rat is only found close to the Colony in the summer, but at that season it overruns many of the houses and is extremely destructive, eating boots, calico, etc., and is especially fond of gnawing the metal spouts of teapots. What becomes of it in winter, I do not know, but I believe it lies dormant under the scrub and brushwood. It never burrows in the ground, but lives under old logs, bushes, etc., and the female makes a nest, generally in the centre of a thick bush or bark stripped into fine shreds and any soft material it can find."

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[1] Its author (Cabrera, 1961, p. 495) now admits that *hypogaeus* is indistinguishable from *Phyllotis griseoflavus medius*, or *P. g. griseoflavus* of my classification. Cabrera also regards *edithae* as identical.

De la Barrera (1936, pp. 439, 720; 1939, p. 441; 1940, p. 565) studied the habits of *P. griseoflavus* in connection with investigations of outbreaks of sylvatic plague in the provinces of La Pampa, Río Negro, and Mendoza, Argentina. According to this authority, *P. griseoflavus*, known locally as *pericote*, lives in every imaginable shelter. In scrub forests of northern La Pampa, the mouse nests in holes in tree trunks and branches. It prefers the *algarrobo* (*Prosopsis alba*) and the *caldén* (*Prosopsis algarrobilla*), the dominant trees of the region. Abandoned nests of many species of birds are also utilized. In the pampas, the nest of an oven-bird, the *cachalote* (*Pseudoseirus*) is a favorite shelter. The nest is the size of a barrel made of loosely interwoven sticks and twigs. *P. griseoflavus* also makes its home under fallen logs, rubbish heaps and brush fences. It commonly nests under the introduced Russian thistle (*Salsola Kali* var. *tenuifolia* Tausch) either at ground level or in a den below the surface. Underground galleries (certainly works of other rodents) are also inhabited by *P. griseoflavus*. In northern Mendoza, the mouse was found living in a state of semi-domesticity in human dwellings. Food of *P. griseoflavus* consists mainly of grains, grasses and fruit of the mesquite *algarrobo* and *caldén*. In Mendoza, de la Barrera was able to recognize the *pericote's* nesting site by the presence of seed husks of peach, thistle and *chañar* (*Gourliea decorticans*, a legume). Seeds of the latter were gleaned by the mouse from goat pellets and carried to the nest for eating.

During the 1937 outbreak of sylvatic plague in Mendoza, de la Barrera (1939, supra cit.) found lactating females in January and February. The number of young recorded for each of 7 nests was, respectively, 9, 10, 8, 7, 8, 7, 8. The same investigator (1940) returned to Mendoza in 1939 and made intensive field studies of rodent carriers of plague. His 9-month record of captured specimens of *Phyllotis griseoflavus* (Table 60) reveals the following phenomena.

1. A minimum of three embryos are developed in *utero;* the average number is 6.

TABLE 60.—*Phyllotis griseoflavus:* Sex ratios and reproduction in specimens captured in northern Mendoza, Argentina (from de la Barrera, 1940, p. 568).

				Adult females		Number of embryos						
Month	Total captured	Males %	Females %	Gravid %	Non-Gravid %	3	4	5	6	7	8	9
February	72	43	57	60.0	39.9	5.8%	11.6%	17.5%	47.3%	11.6%	5.8%	0
March	433	49.8	50.2	64.4	35.6	7.1%	14.3%	14.3%	35.7%	16.2%	12.4%	0
April	116	50.8	49.2	39.8	60.2	0	24.7%	29.5%	45.7%	0	0	0
May	80	51.2	48.8	2.5	97.5	0	0	50	50	0	0	0
June	174	47.1	52.9	0	100	—	—	—	—	—	—	—
July	50	49	51	0	100	—	—	—	—	—	—	—
August	36	61.2	38.8	0	100	—	—	—	—	—	—	—
November	84	47.6	52.4	40.9	59.1	0	5.5%	16.6%	39.1%	22.1%	11.1%	5.5%
December	100	51	49	61.2	38.8	0	6.6%	20.0%	33.3%	26.6%	13.3%	0

2. Most females are gravid in summer (December–March), none in winter (June–August [September?]).

3. The sexes are apparently equal on the basis of a nine-month capture count. Differences in monthly captures between males and females vary from a minimum of 0.4% more females in March, to 22.4% more males in August. The great excess of males over females in August may be attributed, in part, to wider ranging, trap-prone males which were inaugurating the spring breeding season.

According to Kühlhorn (1952, p. 120) females of *P. griseoflavus* from southern Mato Grosso were without young during April and May of 1938. This indicates a reproductive pattern similar to that of the species in Argentina.

In some parts where their geographic ranges overlap, *Phyllotis griseoflavus*, *Phyllotis darwini* and *P. osilae* are found side by side. Other nearly related species occurring in the same areas are *Calomys laucha*, *Calomys carillus*, and *Eligmodontia typus*.

Sylvatic plague in these mice has been recorded by Uriarte and Morales (1935, p. 200) and by de la Barrera (1936, p. 439; 1939, p. 441; 1940, p. 565).

Phyllotis griseoflavus griseoflavus Waterhouse

Mus (*Phyllotis*) *griseo-flavus* Waterhouse, 1837, Proc. Zool. Soc. London, **1837:** 28.

Mus griseo-flavus, Waterhouse, 1839, Zool. Voy. "Beagle," Mamm., p. 62, pl. 21 (animal), pl. 34, fig. 15 (molars)—type redescribed.

Phyllotis griseoflavus, Thomas, 1897, Ann. Mag. Nat. Hist., (6), **20:** 215—ARGENTINA: *Salta* (upper Río Cachi and lower Río Cachi); *Catamarca*. Thomas, 1898, Bol. Mus. Zool. Anat. Comp. Univ. Torino, 13, no. 315: 3—PARAGUAY: *Chaco* (San Francisco Mission).

Hesperomys griseoflavus, Burmeister, 1879, Descr. Phys. Rep. Argentine, **3:** 219—ARGENTINA: Río Chubut to Port Desire.

H[*esperomys* (*Phyllotis*)] *griseoflavus*, Thomas, 1884, Proc. Zool. Soc. London, **1884:** 449—classification.

Eligmodontia griseoflava, Thomas, 1898, Proc. Zool. Soc. London, **1898:** 210—ARGENTINA: *Chubut;* classification; habits. Allen, 1905, Exped. Patag. Princeton Univ., **3**, Mamm., p. 55—review.

Graomys griseo-flavus, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17:** 142—type of *Graomys*.

Graomys griseoflavus griseoflavus, Uriarte and Morales, 1935, Rev. Inst. Bacteriol., **7**, (2): 200, pl. 2 (col.)—ARGENTINA: *La Pampa* (Villasuso); bubonic infection. De la Barrera, 1936, op. cit., pp. 458, 501, fig. 13 (animal), figs. 14–23 (habitats: tree trunks, birds' nests, bushes, etc.)

ARGENTINA: *La Pampa;* bubonic infection. De la Barrera, 1939, op. cit., p. 441, figs. 3, 8, 9 (habitats)—ARGENTINA: *Mendoza* (northeastern part); bubonic infection.

G[raomys] griseoflavus griseoflavus, Yepes, 1935, Rev. Inst. Bacteriol., **7**, (2): 224, pl. 4, fig. 3 (animal)—ARGENTINA: from La Pampa to Santa Cruz.

Hesperomys Bravardi Burmeister, 1879, Descr. Phys. Rep. Argentine, **3**: 228—ARGENTINA: (type locality, Buenos Aires [Pleistocene]).

Phyllotis chacoensis J. A. Allen, 1901, Bull. Amer. Mus. Nat. Hist., **14**: 408—PARAGUAY: *Chaco* (type locality, Waikthlatingwayalwa, northwest of Asunción); ARGENTINA: *Salta* (lower Río Cachi).

E[ligmodontia] chacoensis, Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9**: 132—classification, comparison.

Graomys chacoensis, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 142—classification.

Phyllotis cachinus Allen, 1901, Bull. Amer. Mus. Nat. Hist., **14**: 409—ARGENTINA: *Salta* (type locality, upper Río Cachi).

E[ligmodontia] cachinus, Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9**: 132, footnote—classification.

Graomys cachinus, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 142—classification. Thomas, 1919, op. cit., (9), **3**: 494—ARGENTINA: *Catamarca* (Chumbicha); "*Rioja*" (Otro Cerro). Thomas, 1920, op. cit., (9), **6**: 116—ARGENTINA: *Catamarca* (near Tinogasta). Thomas, 1920, op. cit., (9), **6**: 417—ARGENTINA: *La Rioja* (Potrerillo, Cordillera de Famatina).

Eligmodontia griseoflavus centralis Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9**: 240—ARGENTINA: Córdoba (type locality, Cruz del Eje, 600 meters).

Graomys griseoflavus centralis, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 142—classification.

Graomys sp., Thomas, 1919, Ann. Mag. Nat. Hist., (9), **3**: 116—ARGENTINA: *Catamarca* (Chumbicha).

Graomys medius Thomas, 1919, Ann. Mag. Nat. Hist., (9), **3**: 494—ARGENTINA: *Catamarca* (type locality, Chumbicha, 600 meters). Thomas, 1926, op. cit., (9), **17**: 603—ARGENTINA: *Tucumán* (Tapia). Yepes, 1945, Rev. Argentina Zoogeogr., **4**: 66—ARGENTINA: *Santiago del Estero* (Tacañitas).

Phyllotis griseoflavus medius, Cabrera, 1961, Rev. Mus. argentino Cienc. Nat. "Bernardino Rivadavia," **4**: 495—classification; synonyms, *edithae* Thomas, *hypogaeus* Cabrera.

Graomys lockwoodi Thomas, 1918, Ann. Mag. Nat. Hist., (9), **1**: 187—ARGENTINA: *Salta* (type locality, Manuel Elordi, Bermejo, 500 meters). Thomas, 1920, op. cit., (9), **5**: 191—ARGENTINA: *Jujuy* (Villa Carolina). Thomas, 1926, op. cit., (9), **18**: 194—BOLIVIA: *Potosí* (Tupiza, 2000 meters).

Graomys taterona Thomas, 1926, Ann. Mag. Nat. Hist., (9), **17**: 320—BOLIVIA: *Tarija* (type locality, Tablada, north of Tarija, 2000 meters).

[?]*Graomys* sp., Kühlhorn, 1952, Zeitschr. Säuget., **18**: 120—BRAZIL: *Mato Grosso* (Rio Ivinheima).

Type.—Male, British Museum (Natural History) no. 55.12.24. 184; collected August 1833 by Charles Darwin.

Type locality.—Near mouth of Río Negro, Province of Río Negro, southern Argentina.

Distribution (fig. 103).—From Santa Cruz, Argentina, northward through the Pampas and Chaco into the Chaco region of Paraguay and Bolivia and possibly southern Mato Grosso, Brazil; west into the western foothills of the Andes and Sierras Pampeanas in Argentina; in the departments of Tarija and southern Potosí in Bolivia; altitudinal range from sea level to approximately 2000 meters above.

Characters.—Upper parts of adults buffy to tawny, basal portions of hairs of underparts white to plumbeous; bullae well inflated.

Remarks.—Original measurements for combined head and body length (6″ 8‴ = 169 mm.) and for tail length (5″ 6‴ = 140 mm.) of the type of *Mus griseoflavus* Waterhouse are obviously incorrect and may have been transposed. In this species, the tail is always longer than combined head and body length.

Taxonomy.—*Phyllotis chacoensis* Allen is based on three specimens from the Paraguayan Chaco. They were compared with the type of *griseoflavus* and found to differ by brighter color and hairs of ventral surface wholly white, not "pale plumbeous" basally, as in *griseoflavus*. In 12 adults and subadults from Río Negro, base of hairs of ventral surface vary from white to plumbeous; in 5 juvenals from the same province, the hairs are dark gray basally. In 15 skins from the Paraguayan Chaco, basal portions of hairs of ventral surface are dark gray in one subadult and one adult, pale gray in three adults, and white in ten specimens, including a juvenal and a fully adult cotype of *chacoensis*. Paraguayan Chaco specimens are slightly more warmly colored on dorsal surface than Río Negro representatives of *griseoflavus*. The prominent hair tuft at base of ears described for the holotype of *chacoensis* is absent in the cotype and all other specimens examined. Tail of cotype is well-haired, but without conspicuous pencil.

Phyllotis cachinus Allen from the upper Río Cachi, Salta, was found to be "similar to *griseoflavus* in general coloration but with the pelage of the ventral surface pale grayish at extreme base, instead of *deep plumbeous* [italics mine] for the basal half or more." Variability in color of underparts has already been dealt with. It is of interest to add, nevertheless, that the basal portions of the hairs of the underside of the type of *griseoflavus* appeared to Allen to be "deep plumbeous" in comparison with *cachinus*, and "pale plumbeous" in comparison with *chacoensis*. The specimen that was to become the type of *cachinus* Allen, and another from the lower Río Cachi, Salta, referred by Allen to *chacoensis* had been examined by Thomas (1897, p. 215) who concluded "after the most careful comparison of these Salta specimens with the type [of *Phyllotis griseoflavus* Waterhouse] and with a skin from Catamarca . . . [that he was] still of the opinion . . . that the northern and southern forms cannot be separated."

Eligmodontia griseoflavus centralis Thomas from Córdoba Province, Argentina, was distinguished from all previously described Argentine forms by smaller molars (4.5 mm.) and smaller bullae (6.0 mm.). Size of bullae of *centralis* is less than average, but still well within the range of variation for Argentine *P. griseoflavus*. The molars appear to be extremely small, but measured on the crowns they agree with those of an old adult from Córdoba (MACN No. 29.22). The alveolar length of the molar row is 5.5 mm. in the latter. This specimen also agrees in all other respects with the description and measurements of the type of *centralis*. It cannot be distinguished from northern or southern Argentine representatives of *griseoflavus*.

Phyllotis lockwoodi Thomas from Salta, Argentina, was described as a species with incisors more recurved than in related forms, hind foot larger than in *domorum*, and bullae larger than in *domorum*, smaller than in *chacoensis* and *cachinus*. The form of the incisors is too variable to merit consideration. According to measurements provided by Thomas, hind foot of *lockwoodi* is 32 mm., that of *domorum*, 31. Auditory bullar length of *lockwoodi*, 6.7 mm. according to Thomas, lies well within the limits of variation of specimens from the type region of *cachinus* (6.0–7.3) and from the type region of *chacoensis* (5.9–7.1). It seems that the status of *lockwoodi* is no different from that of other Salta specimens (see *cachinus*, p. 453), so emphatically referred to typical *griseoflavus* by Thomas.

A series of thirty specimens collected by E. Budín in Chumbicha, Catamarca, Argentina, was first recorded as representative of an unidentified species "most nearly allied to *G. chacoensis* and *lockwoodi*." Later, Thomas (1919c, p. 494) discovered to his "surprise . . . that those specimens belong to no less than three species—large, middle, and small,—distinguishable almost entirely by size, though, as is not unusual in such cases, the development of ears, tail, and tail-tufts are in proportion to the general size, the larger species being finer animals throughout, with more handsomely tufted tails. There are no specimens of a size to make determination difficult, and the series of the three species contains examples with fully worn teeth. The largest species, *G. cachinus*, has a skull-length of 33.5–35 mm." The middle-sized species was described as *Graomys medius*. Its skull length is given as 31.2 mm. The smallest species, with skull length 28.5, was called *edithae*. Of the original thirty specimens from Chumbicha, ten were identified as *medius*, six as *edithae*. The remaining 14 specimens were assigned, presumably, to *cachinus*.

In segregating three species on size, Thomas relied on the misleading criterion of a constant and direct relationship between size and age as determined by molar abrasion. The type of variation involved has been discussed under the heading of Crop and Niche Variation (pp. 36, 38).

It will be noted in any case that size difference, admittedly the only difference, between *medius* and specimens Thomas assigned to *cachinus*, allows for practically no individual variation and is, rather, what is expected between individuals of a series as large and representative as the one from Chumbicha. Measurements given for *edithae*, on the other hand, are surprisingly small for an adult and even for a subadult, of the common species. The "supraorbital edges without beading" is also a noteworthy character, whether or not the type of *edithae* is fully adult. Whereas *medius* and *cachinus* are unhesitatingly assigned to the synonymy of *griseoflavus*, judgment on the status of *edithae* must be deferred until the type can be examined. At present, it is listed as a species perhaps nearest related to *Phyllotis hypogaeus* Cabrera.

Since the above was written (prior to 1957) Cabrera (1961, p. 495) has included *edithae* Thomas and *hypogaeus* Cabrera in the synonymy of *Phyllotis griseoflavus medius* on the basis of the following opinion, freely translated: "The small difference in size used by Thomas as basis for distinguishing three species [*edithae*, *medius*, *cachinus*] in a series of otherwise quite similar specimens does not seem to be sufficient grounds for the establishment even of subspecies. The difference seems to be a common population characteristic of frequent occurrence in other kinds of rodents. My *Graomys hypogaeus*, from Corral Quemado, Catamarca, 2250 meters altitude, is indistinguishable from some specimens from a lower elevation in southern Catamarca and which are undoubtedly referable to *medius*."

As already noted, I agree with Cabrera regarding the insignificant difference in size between the Chumbicha specimens determined as *medius* and *cachinus* by Thomas. On the other hand, *edithae* is

TABLE 61.—Measurements of *Phyllotis griseoflavus griseoflavus* Waterhouse

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Bullar length, less tubes	Alveolar length of molar row
PARAGUAY								
Pto. Casado	165,165,128	185,145,164	33,30,27	—, —, —	36.8,37.3,31.7	18.1,18.4,16.2	6.9,7.1,6.2	6.0,5.9,5.1
Colonia Fernheim	111,124	164,151	30,31	—, —	34.4,33.7	16.5,16.9	6.5,6.8	5.8,5.8
Guachalla	135,115,122, 135	175,141,168, 155	26,29,29,28	—, —, —, —	33.0,30.8,34.6, —	15.9, —,17.5, —	6.2,6.0,6.2, —	5.3,5.1,5.2,5.2
Waikthlating-wayalwa[1]	142	185	33	24	38	18	—	5.0[2]
Waikthla-waya[3]	?	114	27	20	31.8	16.2	5.5	5.7
BOLIVIA								
Río Pilco-mayo	142	150	30	—	33.5	16.7	5.5	5.7
Guanacos	150,110	170,140	28,27	28,20	31.2,34.1	15.9,17.9	6.1,6.4	5.4,5.3
Tarija	131	150	30	26	—	—	5.9	5.5
Tablada[4]	152	161	30	25.5	38	19	—	5.4
ARGENTINA								
Río Negro[5]	169	140	30.8	16.8	—	—	—	—
Chubut	130	166	28	25	—	—	—	—
Chimpay	144,137,138	149,151,134	31,30,31	—,—,—	34.0,32.5,31.9	16.9,16.5,15.9	7.0,6.9,6.6	6.1,5.4,5.0
Choele-Choel	122	137	27	23	31.7	—	5.9	5.4
Cruz del Eje[6]	130	156	29	26	33.5	17	6.0	4.5[2]
La Paz	130	160	28	25	34.2	—	7.0	5.5

TABLE 61.—Measurements of *Phyllotis griseoflavus griseoflavus* Waterhouse (*concluded*)

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Bullar length, less tubes	Alveolar length of molar row
San Juan	123,135,149	117,160, —	29,29,27	21,25,22	31.6,32.4,34.4	16.4, —,17.3	6.2,7.8,7.8	5.5,5.6,5.7
Corral Quemado	—, —	—, —	—, —	—, —	35.5,33.6	18.7,17.3	7.7,7.1	6.4,5.5
Belén	138,119,118, 129	158,143,140, 171	27,28,27,28	25,25,25,24	33.3,33.3,31.7, —	17.2,17.2,15.6,16.2	7.0,7.6,6.9,7.0	5.7,5.9,5.6,5.7
Chumbicha[7]	124	150	27	25	31.2	16.1	6.4	5.2
Lavalle	122(106-139)14	146(125-190)14	28(25-31)14	23(21-25)14	31.6(29.6-33.7)8	16.6(15.5-18.3)10	6.1(5.5-6.6)10	5.3(5.1-5.5)11
El Desmonte	106	139	26	23	—	—	6.0	5.5
Río Cachi[8]	137	159	29	24	35.0	17	7.3	5.4
Macapillo	134	172	27	25	34.3	—	6.5	5.2
La Represa	126	136	27	22	32.2	17.0	6.3	5.1
Manuel Elordi[9]	131	150	32	25	35	18	6.7	5.4
Las Palmas	152	165	34	27	35.3	18.4	6.7	5.9

[1] Type of *chacoensis* Allen, from original description.

[2] Crown length.

[3] Juvenal.

[4] Type of *laterona* Thomas, from original description.

[5] Type of *griseoflavus* Waterhouse, from original description.

[6] Type of *centralis* Thomas, from original description.

[7] Type of *medius* Thomas, from original description.

[8] Type of *cachinus* Allen, from original description.

[9] Type of *lockwoodi* Thomas, from original description.

distinguished not only by an appreciable difference in size, but by a cranial character which should not be dismissed without good reason. I am also unwilling to accept at face value Cabrera's identification of his *hypogaeus* with *Phyllotis griseoflavus*. Some explanation of what would now be regarded as serious errors in the description of the type and depiction of its molars (cf. fig. 107) is in order.

Graomys taterona Thomas from the Bolivian headwaters of the Río Bermejo is indistinguishable in external characters from Río Pilcomayo mice already described as *chacoensis* (=*griseoflavus*). The bullae of the type of *taterona* were said to be smaller than in *lockwoodi* and *chacoensis,* larger than in *domorum*. No measurements were given in support of the statements. Two specimens of the ten composing the original type series are at hand. Their skulls are badly damaged but bullae, intact in one, a fully developed adult, measure 6.0 mm. The length indicates an intermediate position between *griseoflavus* and *domorum*. On a geographic basis, however, the type of *taterona* is best assigned to *griseoflavus.*

Measurements.—See Table 61.

Specimens examined.—78. ARGENTINA.—*Chubut:* Rawson, 1 (MACN); *Río Negro:* Chimpay, 9 (CNHM); Choele-Choel, 5 (MACN, 2; CNHM, 3); Pichi Mahuida, 1 (CNHM); *Buenos Aires:* Algarrobo, 1 (MACN); *Córdoba:* La Paz, 2 (MACN); *San Juan:* Media Agua, 3 (AMNH); *La Rioja:* General Roca, 2 (MACN); *Tucumán:* Tapia, 1 (MACN); *Catamarca:* Chumbicha, 1 (CNHM); Puntilla, Tinogasta, 2 (CNHM); Belén, 6 (CNHM); *Santiago del Estero:* Lavalle, 16 (AMNH); *Salta:* El Desmonte, Metán, 4 (MACN, 3; CNHM, 1); Macapillo, Metán, 2 (MACN); La Represa, Metán, 1 (CNHM); *Chaco:* Avia Terai, 1 (AMNH); Las Palmas, 1 (MACN). PARAGUAY.—*Chaco:* La Urbana, 1 (CNHM); Jesematathla, 1 (CNHM); Colonia Fernheim, 2 (CNHM); Guachalla, 5 (CNHM); Puerto Casado, 3 (CNHM); Waikthlatingwayalwa, 1 (AMNH); Waikthlawaya, 1 (AMNH). BOLIVIA.—*Santa Cruz:* Guanacos, 2 (CNHM); *Tarija:* Tablada, 2 (CNHM). *?Department:* Río Pilcomayo, 1 (AMNH).

Phyllotis griseoflavus domorum Thomas

Eligmodontia domorum Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9**: 132. Thomas, 1902, op. cit., (7), **9**: 223—BOLIVIA: *Sucre* (Sucre); *Potosí* (El Cabrado).

E[*ligmodontia*] *g*[*riseoflavus*] *domorum,* Thomas, 1902, Ann. Mag. Nat. Hist., (7), **9**: 240—comparison.

Graomys domorum, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 142—classification.

Phyllotis (*Graomys*) *domorum*, Osgood, 1916, Field Mus. Nat. Hist., Zool. Ser., **10**: 207—BOLIVIA: Parotani, Cochabamba.

Type.—Adult male, British Museum (Natural History) no. 1.1.1.47; collected 23 March, 1901, by Perry O. Simons.

Type locality.—Tapacari, at headwaters of Río Rocha, about 50 kilometers southwest of Cochabamba, Department of Cochabamba, Bolivia; altitude, approximately 3000 meters above sea level.

Distribution (fig. 103).—Bolivian highlands, from the headwaters of Río Arque in the Lake Poopo drainage basin eastward into the Río Grande (upper Río Mamoré) drainage basin, departments of Cochabamba and Santa Cruz; altitudinal range, from approximately 2000 to about 3000 meters above sea level.

Characters.—Color of upper parts of adults from olivaceous, as in juvenals of typical *griseoflavus*, to rufous; hairs of ventral surface dark basally; bullae comparatively small, their average antero-posterior length, less tubes, approximately equal to average length of molar row.

Variation.—There are no significant differences between specimens from the Río Grande on the Amazonian slope of the Cordillera Real and specimens from the upper Río Arque in the Lake Poopo basin across the divide.

Taxonomy.—The original series of *domorum* was distinguished from other representatives of the species by "less bushy tail and smaller bullae." Degree of hairiness of tail varies individually and seasonally. On the other hand, bullae in 3 specimens from Parotani, a locality in the type region, are less inflated than in representatives of the nominate race. In the vast majority of specimens of *P. g. domorum*, the antero-posterior length of bullae, less tubes, is less than alveolar length of molar row.

In connection with his description of *domorum*, Thomas remarked that "the most interesting point about this species is its extraordinary resemblance to *Phyllotis Wolffsohni*, caught at the same localities. Except that the *Eligmodontia* [i.e., *domorum*] has larger and clumsier feet, it is almost impossible to distinguish the two without examining the skulls. This resemblance in itself is a point in favour of the two animals being really generically different[!]"

Measurements.—See Table 62.

Table 62.—Measurements of *Phyllotis griseoflavus domorum* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Bullar length, less tubes	Alveolar length of molar row
Tapacari[1]	140	146 (to 170)[2]	31 (from 29)[2]	25	35.4	18.4	—	5.1
Parotani	132(102–150)18	147(120–166)18	30(28–32)18	21(20–25)15	33.3(32.0–34.8)12	16.7(15.5–17.5)11	5.5(5.3–6.1)12	5.6(5.4–5.9)16
Tin Tin	135	145	28	27	33.5	—	5.6	5.6
Aiquile	115,120	140,165	26,27	25,26	32.4,34.3	16.7,17.1	5.4,6.0	5.2,6.0
Comarapa	140	160	29	23	33.0	–	5.8	5.3

[1] Type, from original description.

[2] Extremes *ex* Thomas, from original description.

Specimens examined.—43. BOLIVIA.—*Cochabamba:* Parotani, 33 (AMNH, 31; CNHM, 2); Tin Tin, 5 (CNHM); Aiquile, 3 (CNHM); *Santa Cruz:* Comarapa, 1 (CNHM); Florida, 1 (CNHM).

Phyllotis edithae Thomas

Graomys edithae Thomas, 1919, Ann. Mag. Nat. Hist., (9), 3: 495.

Type.—Male, British Museum (Natural History), no. 19.2.7.34; collected 26 September, 1918, by E. Budín.

Type locality.—Otro Cerro, a collecting locality about 18 kilometers NNW of Chumbicha, Catamarca, Argentina; altitude, 3000 meters above sea level.

Distribution (figs. 57, 108).—Known only from the type locality in the Andes of northern Argentina.

Characters.—The original description follows: "Size again smaller than in *G. medius*, making it the smallest known species of the genus [*Graomys*]. Colour about as in that animal, a buffy wash on the sides rarely present. Under surface white, the hairs either slaty basally or white to their roots. Tail shorter than in *medius*, and less heavily haired terminally; brown above, white on sides and below.

"Skull a miniature of that of the other species; supraorbital edges without beading.

"Dimensions of the type:—

"Head and body 108 mm.; tail 127; hind foot 25; ear 20.

"Skull: greatest length 28.5; condylo-incisive length 26.5; zygomatic breadth 15; nasals 10.5; interorbital breadth 4.5; breadth of braincase 13.5; palatilar length 12.8; palatal foramina 6.7; length of bullae 6; upper molar series 4.7."

Remarks.—*P. edithae* was described as the smallest species of the group typified by *P. griseoflavus*. As a species of *Phyllotis*, however, it is larger than *P. hypogaeus, gerbillus* and *amicus*. Absence of supraorbital beading in the skull of *edithae* is also a character of *gerbillus* and *amicus*. The status of *edithae* must remain obscure until the enamel pattern of its molars can be studied.

In addition to the type from Otro Cerro, Thomas recorded 6 specimens from Chumbicha, Catamarca. They were taken together with representatives of *cachinus* and *medius*, both synonyms of *P. griseoflavus griseoflavus*. The possibility that *edithae* may also be a synonym is discussed above (footnote 1, p. 448, and p. 455).

Specimens examined.—None.

Phyllotis hypogaeus Cabrera[1]

Graomys hypogaeus Cabrera, 1934, Notas Prelim. Mus. La Plata, **3**, (1a): 124, fig. (molars).

Type.—Adult male, Museo de La Plata, Universidad de La Plata, Buenos Aires; collected 25 February, 1930, by Angel Cabrera.

Type locality.—Corral Quemado, Belén, Catamarca; altitude 2250 meters above sea level.

Distribution (figs. 57, 108).—Known only from type locality in the Andes of northern Argentina.

Characters.—The original description, translated from the Spanish, follows: "Size less than in any other known species of *Graomys;* pelage of upper parts pinkish buff with a grizzling on the back and forehead, the hairs slaty basally; underparts and feet white, the hairs white to the roots; a white postauricular patch present as in *Eligmodontia typus* and *Hesperomys bimaculatus.* Pencilled tail white with tawny-olive stripe on upper surface, the stripe sharply defined, nearly black at terminal portion, but hardly distinguishable basally.

"Skull with interorbital region expanded behind, the edges finely ridged; anterior border of zygomatic plate slightly concave, the upper corner projecting. Molars similar to those of *Phyllotis darwini.*

"Measurements: Head and body, 80 mm.; tail, 114; hind foot, 23; ear, 18; greatest length of skull, 23; condylobasal length, 22; zygomatic breadth, 13.5; interorbital constriction, 4; palatilar length, 10.3; palatine foramina, 5.5; nasals, 8; auditory bulla, 4.5; diastema, 6; upper molar row, 3.6; lower molar row, 4.

"This mouse, apparently the smallest species of the genus *Graomys,* resembles *G. edithae* Thomas of southeastern Catamarca (type locality, Otro Cerro, eastern slope of the Sierra de Ambato) but is smaller, its sides with a buffy wash not present in *edithae,* and tail with a well developed pencil. It resembles *Eligmodontia typus* superficially, but differs in the structure of the molars, and by its naked soles and pencilled tail."

Habits and habitat.—The type of *P. hypogaeus* was discovered by Cabrera living among the large stones inside the tombs of prehistoric Indians. Nests of the mice were nearly spherical in shape and formed of dry grasses. The natives call the little animal *raton punero.* The region around Corral Quemado is described as arid, the sandy soil supporting xerophytic vegetation with many *car-*

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[1] See footnote, p. 448.

dones. Phyllotis griseoflavus and *Eligmodontia typus* live in the same locality.

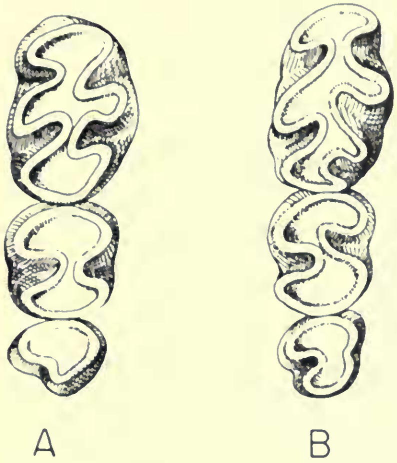


FIG. 107.—Molars of *Phyllotis hypogaeus* (after Cabrera): A, left upper; B, left lower.

Remarks.—The mouse described by Cabrera may be unique. The enamel pattern of the molars (fig. 107) of *P. hypogaeus* is like that of comparably worn molars of *Phyllotis darwini.* The described cranial characters, however, agree with those of *P. griseoflavus*, or possibly *P. amicus.* Measurements indicate *hypogaeus* may be the smallest species of *Phyllotis.* Characters of color of sides of body and degree of hairiness of tail adduced by Cabrera for distinguishing *hypogaeus* from *edithae* are individual variables and conflict with statements in the original description of the latter. On the other hand, edges of supraorbital region of *hypogaeus* are described as finely ridged or beaded, while those of *edithae* are said to lack beading.

Taxonomy.—In his posthumously published second part of the *Catálogo de los mamíferos de America del Sur,* Cabrera (1961, p. 495) disposes of his *hypogaeus* (and *edithae* Thomas) in the synonymy of *Phyllotis griseoflavus medius.* This action carried with it no explanation for certain diagnostic characters attributed to *hypogaeus* which are opposed to those of *Phyllotis griseoflavus.* For additional comments see *Phyllotis griseoflavus griseoflavus.*

Specimens examined.—None.

Genus **Galenomys** Thomas

Galenomys Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 143—subgenus of *Euneomys* Coues. Gyldenstolpe, 1932, K. Sv. Vet. Akad. Handl., **11**: 96—full genus. Ellerman, 1941, The families and genera of living rodents, **2**: 451, 452, 455—subgenus of *Phyllotis*. Osgood, 1947, Journ. Mamm., **28**: 171—subgenus of *Phyllotis*.

[*Galenomys*], Thomas, 1926, Ann. Mag. Nat. Hist., (9), **17**: 317—former subgenera of *Euneomys* regarded as full genera.

Type species.—*Phyllotis garleppi* Thomas, by original designation.

Included species.—*Galenomys garleppi* Thomas.

Distribution

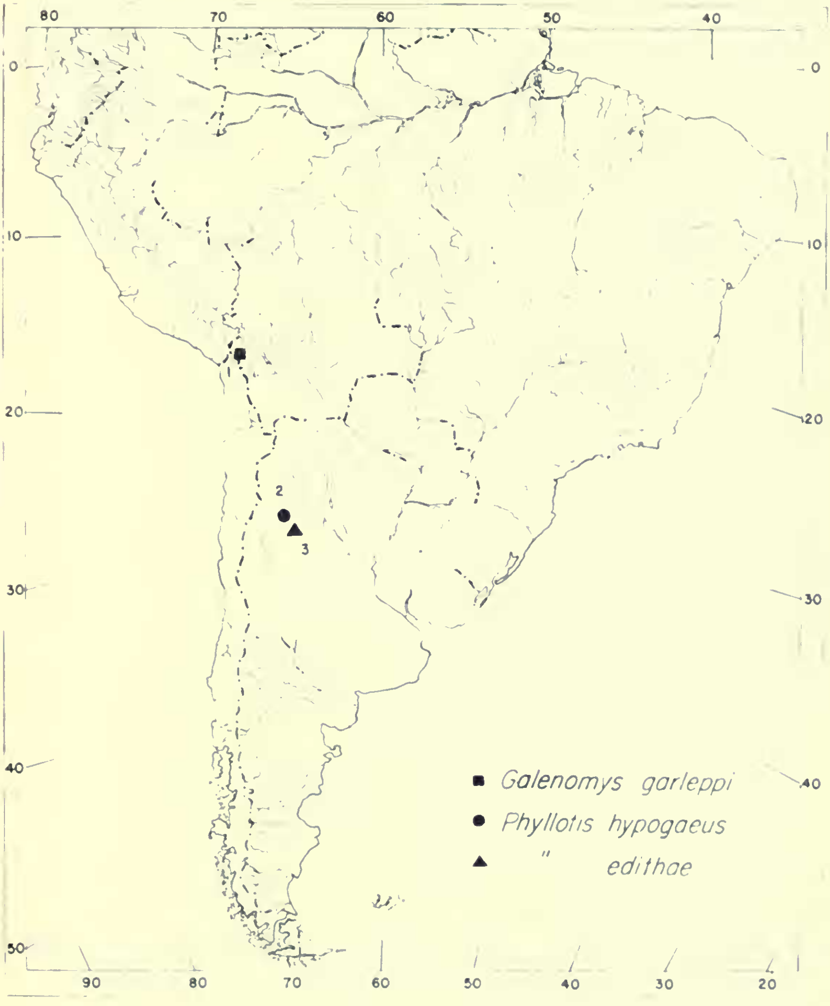
Figures 52, 108

The altiplano of western Bolivia, southern Peru and extreme northeastern Chile.

Characters

External.—General appearance vole-like, color pale, size medium, body stout, tail short; upper parts of trunk buffy thinly lined with brown, sides clearer, rump ochraceous, head paler than trunk; underparts and legs sharply defined white, the individual hairs wholly white on legs, feet, hands and chin to anterior part of chest, slaty basally on remaining underparts; ears large, well haired on outer side; fore and hind feet white above, hind feet (fig. 3) beneath thinly covered with long white hairs except on tubercles and terminal phalanges; tail from approximately one-third to nearly one-half combined head and body length, thickly haired white above and below, the scales not visible, terminal tuft not conspicuous.

Cranial (figs. 61–63, 109, 110).—Dorsal contour of skull extremely arched, rostrum inflected downward, its dorsal plane forming an angle of about 30 degrees with plane of frontals; supraorbital region narrow, constricted mid-frontally, the edges square, not ridged or beaded, interparietal moderately developed; zygomatic arches delicate, as widely expanded anteriorly as posteriorly and with a pronounced downward inflexion; fronto-parietal sutures crescentic in outline, not forming an angle at midline, distance across sutures on dorsal surface more than greatest width across fronto-maxillary sutures and more than alveolar length of molar row; anterior zygomatic plate nearly as wide as least interorbital breadth, the anterior border straight and slanted backward, upper anterior corner rounded; palate arched in conformity with dorsal curvature of skull, its width between first molars more than length of m^1; incisive foramina com-


80
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3
■ Galenomys garleppi
● Phyllotis hypogaeus
▲ " edithae
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30
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FIG. 108. Type localities of *Galenomys garleppi*, *Phyllotis hypogaeus* and *P. edithae:* 1, Esperanza, Mount Sajama, La Paz, Bolivia; 2, Corral Quemado, Belén, Catamarca, Argentina; 3, Otro Cerro, Catamarca, Argentina.

paratively well opened, especially posteriorly; pitted posterolateral palatal depressions shallow; mesopterygoid fossa narrow, its width at anterior base of pterygoid processes less than width of $m^{\underline{3}}$ or about one-half width of parapterygoid fossa measured at same plane; bullae moderately inflated, length, less tubes, less than alveolar length of molar row.

Dental (figs. 62, 63, 69, 111).—Incisors delicate, ungrooved, forward projecting, the lower remarkably procumbent; upper molar rows bowed outwardly; upper and lower first molars 4-rooted; crowns low, slightly terraced, cusps ovate; second and third upper molars each at least as wide as long, anteroloph of second moderately developed, of third weak; postcingulum absent in worn upper molars, present in lower; minor fold present in lower first and second molars, absent in worn uppers.

Comparisons

Superficially, *Galenomys* most nearly resembles pale individuals of *Phyllotis sublimis.* It is distinguished by relatively shorter, more thickly haired tail, and stouter hind feet with hairy soles. In the smaller, longer-tailed *Eligmodontia,* the thickly haired part of the sole is restricted to the surface of the three coalesced middle postdigital tubercles. In contrast the plantar tubercles of *Galenomys* are bare and not fused. *Galenomys* also resembles *Phyllotis sublimis* in cranial characters, but the downwardly flexed rostrum and low-slung zygomatic arches of the first occur in no other phyllotine. The skull of the sigmodont *Reithrodon* is comparable in outline but the dorsal contour is evenly convex, or leporine, not abruptly bent downward at rostrum; the zygomatic arches are almost as low as in *Galenomys,* but slightly more expanded posteriorly than anteriorly, the orbits much larger. Because of the inward rotation of $m^{\underline{3}}$, the appearance of outward bowing of the upper molar rows is extreme in *Galenomys.* Otherwise, the molars are similar to those of *P. sublimis,* but relatively wider. The lower incisors of *Galenomys* attain a degree of procumbency not equaled in any other living cricetine. However, in *Bensomys* Gazin of the Kansas Pleistocene, the lower incisors are similarly procumbent, and the lower molars show the same enamel pattern as in *Galenomys.*

The equally short-tailed, vole-like *Punomys lemminus* Osgood bears a superficial resemblance to *Galenomys garleppi.* Both species inhabit the altiplano and possibly may occur in the same parts. *Punomys* is larger, darker in color, its hind feet with but a few scat-

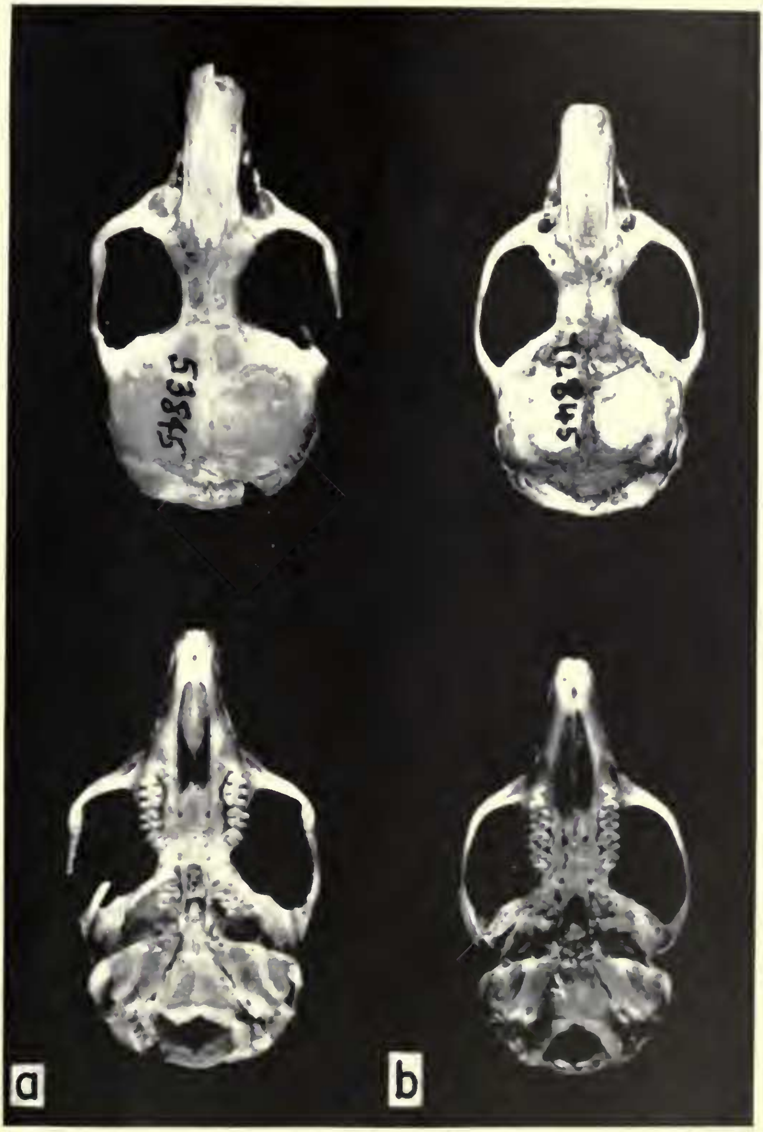

53845
12845
a
b

FIG. 109. – Dorsal and ventral aspects of skulls of *a*, *Galenomys garleppi*; *b*, *Phyllotis sublimis*. (about × 2.)

tered hairs between the plantar tubercles, ears considerably shorter, tail bicolor. Cranially, *Punomys* is intermediate between *Phyllotis* and sigmodont rodents; the enamel pattern of its molars, however, is unique.

Taxonomy

The vaulted skull, low slung, anteriorly expanded zygomata, enlarged first upper molars, uniquely procumbent lower incisors, extremely hairy soles and very short, hairy tail are individually distinctive characters that together justify generic rank for *Galenomys*. None of the species heretofore referred to as *Auliscomys*, erstwhile subgenus of *Phyllotis*, show such absolute distinctions. Each of them is distinguished from all other species of *Phyllotis* by relative differences and by the manner in which common characters are combined. *Phyllotis sublimis* appears to be nearest related to *Galenomys*.

When first described, *Galenomys garleppi* was doubtfully referred to *Phyllotis*. It was compared with grasshopper mice of the genus *Onchomys* because of a superficial resemblance. In 1916, Thomas reclassified some South American Muridae and erected *Galenomys* as one of three subgenera of *Euneomys*. In 1926, however, Thomas decided that the "three subgenera into which *Euneomys* has been divided, largely on Mr. Osgood's work, being unnatural groups, I propose to consider them as full genera, as this course is so far more *convenient both for labelling and reference*" [italics mine]. Ellerman (1941, supra cit.) and Osgood (1947, supra cit.) preferred to regard *Galenomys* as a subgenus of *Phyllotis*.

Galenomys garleppi Thomas

Phyllotis (?) *Garleppii* Thomas, 1898, Ann. Mag. Nat. Hist., (7), **1**: 279.

Euneomys (*Galenomys*) *garleppi*, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 143—type of subgenus.

Galenomys garleppii, Gyldenstolpe, 1932, K. Sv. Akad. Handl., **11**: 96—description.

Phyllotis [(*Galenomys*)] *garleppii*, Ellerman, 1941, The families and genera of living rodents, **2**: 452, 455. Osgood, 1947, Journ. Mamm., **28**: 171.

Phyllotis (*Galenomys*) *garleppi*, Pearson, 1957, Breviora, Mus. Comp. Zool., no. 73: 2, fig. 1 (skull)—PERU: *Puno* (Pichupichuni, 5 miles northwest of Huacullani, 12,600 feet; Pampa de Ancomarca, 76 miles south of Ilave, 13,700 feet).

Type.—Adult male, skin and skull, British Museum (Natural History), no. 98.3.16.5; collected May 20, 1897, by Gustav Garlepp.

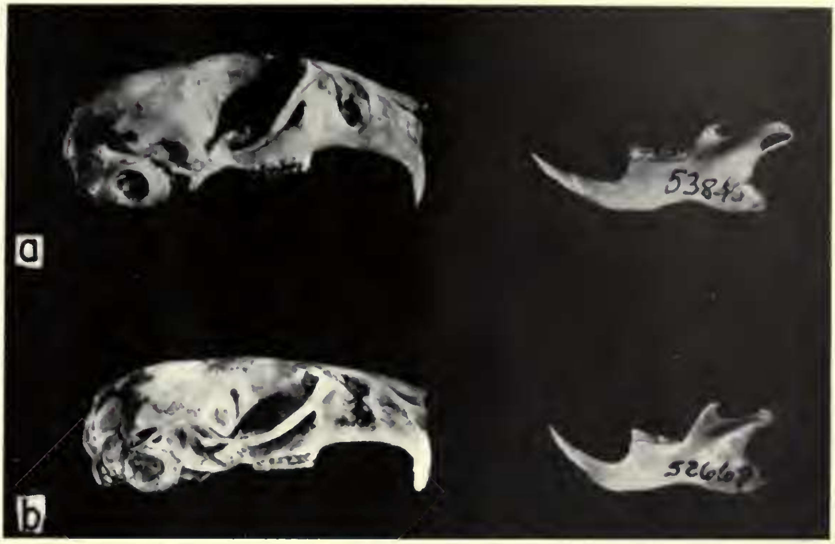


FIG. 110.—Side view of skull of *a*, *Galenomys garleppi*; *b*, *Phyllotis sublimis*. (about × 1½.)

Type locality.—Esperanza, Mount Sajama, Pacajes Province, La Paz, Bolivia; altitude, 4000 meters above sea level.

Distribution (figs. 52, 108).—The puna zone in the departments of La Paz, Bolivia, Puno, Peru, and bordering parts of Tarapacá, Chile; altitudinal range from approximately 3800 to 4500 meters above sea level.

Characters.—The characters of the species are those of the genus. The mammae of a female at hand are not sufficiently developed for determination of their number. The type is said to be a male, but Gyldenstolpe (supra cit.) gives the mammary formula for *Galenomys* as $2-2=8$.

Remarks.—The procumbent lower incisors of *Galenomys* recall those of insectivores and caenolestids while the downwardly bent rostrum is comparable to the condition in the cuniculoid *Reithrodon* as well as to that in leporids in general. Nothing is known of the habits of *G. garleppi*.

Galenomys garleppi is known from the type, another Bolivian specimen in the British Museum (Natural History), the specimen at hand in Chicago Natural History Museum, and two specimens in the Museum of Vertebrate Zoology, Berkeley, California. The latter were collected and recorded by Pearson (supra cit.) while this paper was in press.

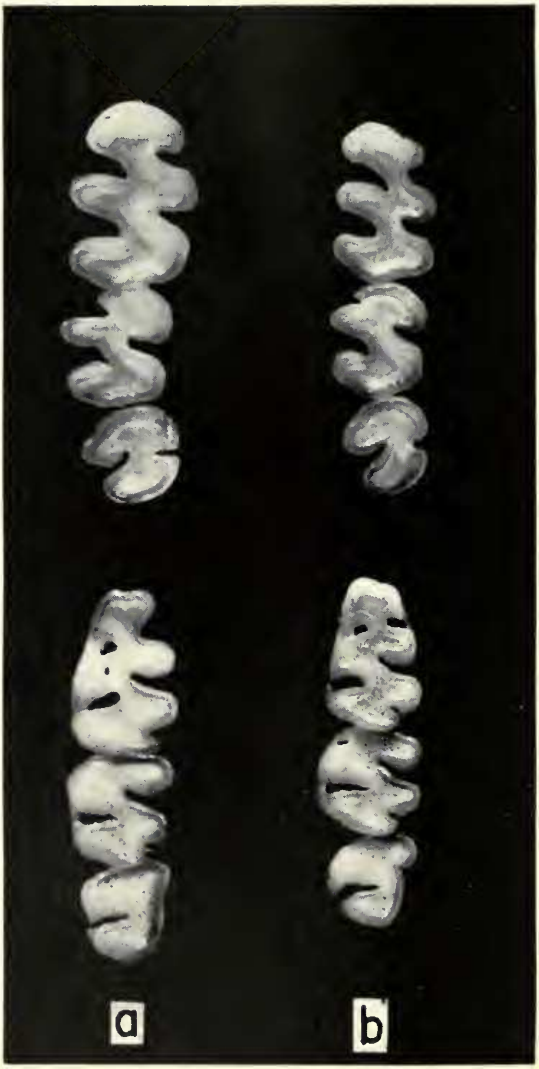
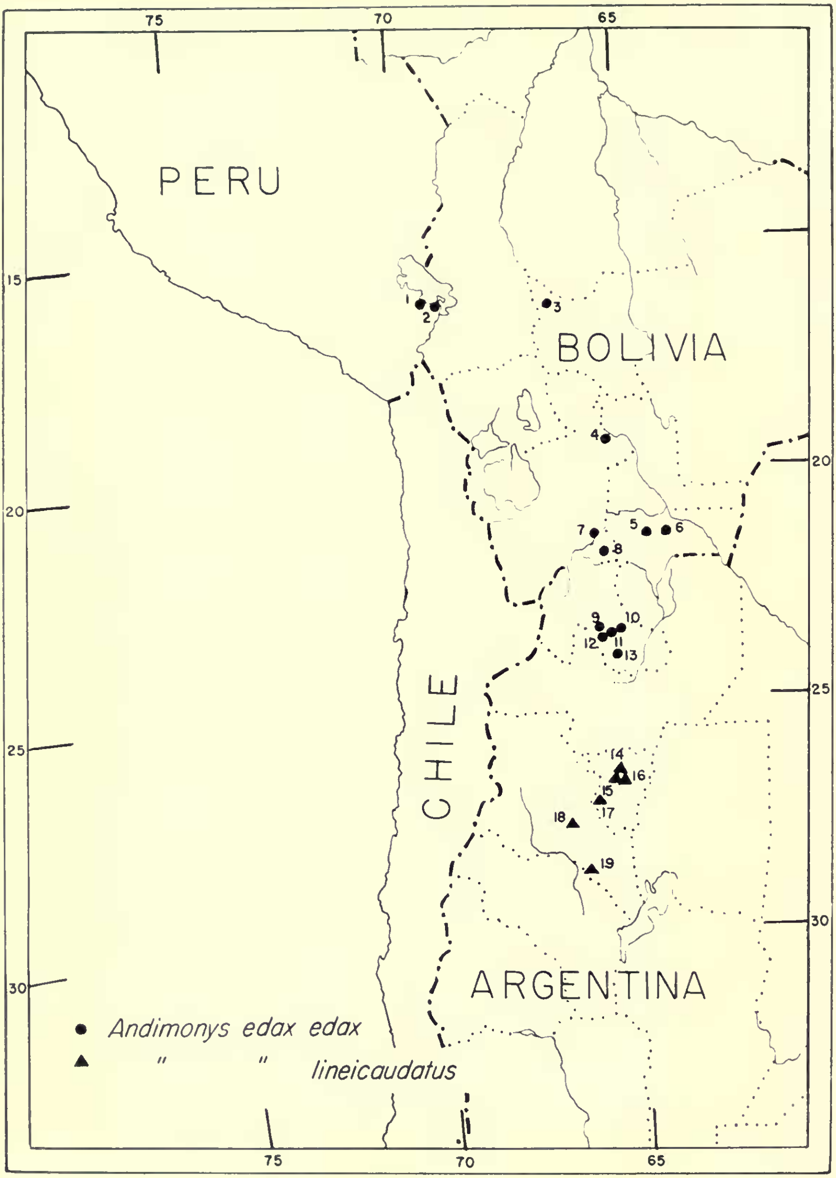


FIG. 111.—Right upper and left lower molars of *a*, *Galenomys garleppi*; *b*, *Phyllotis sublimis.*

Measurements.—Those of the type, a male, from original description followed by those of a female topotype: head and body, 123 (from dry skin), 105; tail, 38 (from dry skin), 45; hind foot, 25 (dry), 25 (dry, with claw); greatest length of skull, —, 30.2; zygomatic breadth, 17.8, 16.7; nasals, 13.4, 13.1; interorbital constriction, —, 3.9; braincase, —, 13.9; zygomatic plate, width, —, 3.3; bulla, length less tube, —, 5.0; incisive foramina, 7.2, 6.8; diastema, 8.7, 8.6; alveolar length of upper molar row, 5.1, 5.3.

Specimens examined.—1. BOLIVIA. *La Paz:* Esperanza, 1 (CNHM).



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● Andimonys edax edax
▲ " " lineicaudatus

Fig. 112.—Collecting localities of the subspecies of *Andinomys edax*. See opposite page for explanation.

Genus **Andinomys** Thomas

Andinomys Thomas, 1902, Nature, **65**: 431 (6 March)—abstract. Thomas, 1902, Proc. Zool. Soc. London, **1902**: 116 (June, *apud* Duncan, 1937, Proc. Zool. Soc. London, (A), 107: 75). Yepes, 1935, Anal. Mus. argentino Cienc. Nat., **38**: 333—revision. Osgood, 1947, Journ. Mammal., **28**: 173—characters, comparisons.

Type species.—Andinomys edax Thomas, by original designation.

Included species.—Andinomys edax Thomas.

Distribution

Figures 52, 112

Highlands of southern Peru, Bolivia and northwestern Argentina.

EXPLANATION OF FIGURE 112

Andinomys edax: collecting localities and collectors.
Type localities in **boldface**.

Andinomys edax edax (1–13)

PERU (1–2)

1. Juli, Lake Titicaca, Puno.—O. P. Pearson at 12,500 feet.
2. Yunguyo, 6 miles south, Puno.—C. C. Sanborn at 13,000 feet.

BOLIVIA (3–8)

3. Choro, Cochabamba.—J. Steinbach at 3500 meters.
4. **El Cabrado.**—P. O. Simons at 3700 meters.
5. Sama, Tarija.—E. Budín at 4000 meters.
6. Piños, Tarija.—E. Budín.
7. Tupiza, Potosí.—E. Budín at 2000 meters.
8. Yuruma (Estancia), Potosí.—E. Budín at 2200 meters.

ARGENTINA (9–13)

9. Cerro Casabindo, Jujuy.—E. Budín at 4800 meters.
10. Sierra de Zenta, Jujuy.—E. Budín at 4500 meters.
10. La Laguna, Sierra de Zenta, Jujuy.—E. Budín at 4500 meters.
11. Maimará, Jujuy (2230 meters).—E. Budín.
11. Alfarcito, near Maimará, Jujuy.—E. Budín at 2600 meters.
12. Cerro La Lagunita, Maimará, Jujuy.—E. Budín at 4500 meters.
13. Yala, mountains west of, Jujuy.—W. H. Osgood.

Andinomys edax lineicaudatus (14–19)

ARGENTINA

14. Ñorco, Vipos, Tucumán.—E. Budín at 2500 meters.
15. **Cerro San Javier, Tucumán.**—E. Budín at 2000 meters.
16. Sierra de Tafí Viejo, Tucumán.—E. Budín at 2000 meters.
17. Aconquija, Tucumán.—J. Mogensen at 3000 meters.
18. Río Vallecito, Catamarca.—J. Crespo.
19. Otro Cerro, Catamarca.—E. Budín at 3000 meters.

Characters

External.—Large, heavy-bodied, pelage soft, lax, upper parts and sides of body drab, underparts gray, the slaty bases of the hairs showing through, tail from 60 per cent to approximately equal to head and body length, sharply bicolor, thinly haired and without terminal brush; fore and hind feet well developed, white above; heel well haired, plantar surface bare, the tubercles greatly enlarged but not fused; ears comparatively small, usually with a fine gray edging; mammae, 2−2=8.

Cranial (figs. 61, 63, 113).—Dorsal surface of skull flattened; supraorbital region narrow, parallel-sided, the edges square or slightly raised; a slit-like fontanelle present between anterior halves of frontals. A second fontanelle sometimes present between posterior ends of frontals; temporal ridges obsolete or absent; interparietal well developed; zygomata moderately expanded, markedly wider posteriorly than anteriorly; fronto-parietal sutures meeting at midline to form a right or acute angle, distance across them on dorsal surface less than greatest width across fronto-maxillary sutures and less than alveolar length of molar row; nasals broad posteriorly, well expanded anteriorly; anterior border of zygomatic plate straight or slightly concave, the upper border pointed or projecting as a short process; incisive foramina comparatively well-open, elliptical in outline; bony palate narrow anteriorly, and barely extending behind to posterior plane of third molar; greatest width between inner borders of first molars less than greatest length of $m\frac{1}{}$; pitted posterolateral palatal depressions troughlike, continued as gutters on anterolateral portion of palate; mesopterygoid fossa comparatively broad, width at anterior base of pterygoid processes nearly equal to width of parapterygoid fossa measured at same plane; parapterygoid fossae shallow, especially anteriorly; bullae moderately inflated, length, less tubes, less than length of molar row.

Dental (figs. 19, D, 63, 69, 114–116).—Upper incisors opisthodont, broad, ungrooved, external surface flexed inwardly toward midline to form a broad median valley, cutting edges meeting to form an approximately 90° angle, upper molar rows divergent posteriorly; upper first molar 3-rooted, lower 2-rooted; molars large, prismatic, flat-crowned; cusps of $m\frac{1-2}{1-2}$ triangulate; crown of $m\frac{3}{}$ involuted in unworn, roughly 8-shaped in worn, of $m_{\overline{3}}$ fused on lingual side; procingulum of $m\frac{1}{}$ subtriangular, the primitive trilobate pattern hardly or not at all indicated; first primary fold of $m\frac{2}{}$ well developed and persistent in adult, of $m\frac{3}{}$ reduced to an enamel island in newly erupted and obso-

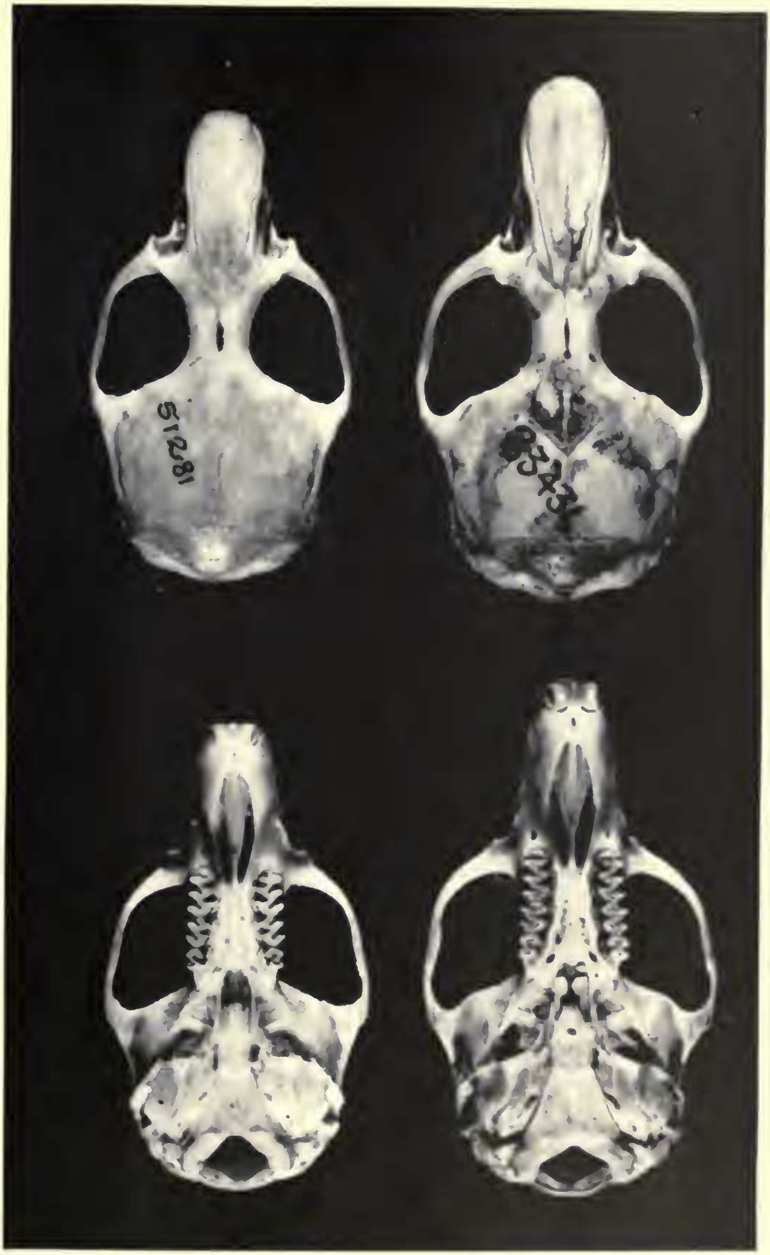
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FIG. 113.—*Andinomys edax*. Dorsal and ventral aspects of skull. Note frontal fontanelles. (About × 2.)

lete in slightly worn tooth; second primary fold of $m^{\underline{1-2}}$ extending little or not at all beyond longitudinal midline of molars; postcingulum obsolete in $m^{\underline{1-2}}$, vestigial in juvenal $m^{\underline{3}}$; first minor fold indicated in $m^{\underline{3}}$, slightly more developed in $m^{\underline{2}}$; inner and outer cusps of first and second molars subequal; procingulum of $m_{\overline{1}}$ trilobate in juvenal, bilobate with anterior median fold persistent in adult; first minor fold well developed in $m_{\overline{2}}$, shallower in $m_{\overline{3}}$; apices of major and first primary folds of $m_{\overline{1-2}}$ touching; second primary fold of $m_{\overline{2}}$ short, extending about one-fourth distance across molar crown; first primary fold of $m_{\overline{3}}$ nearly obsolete, second primary absent.

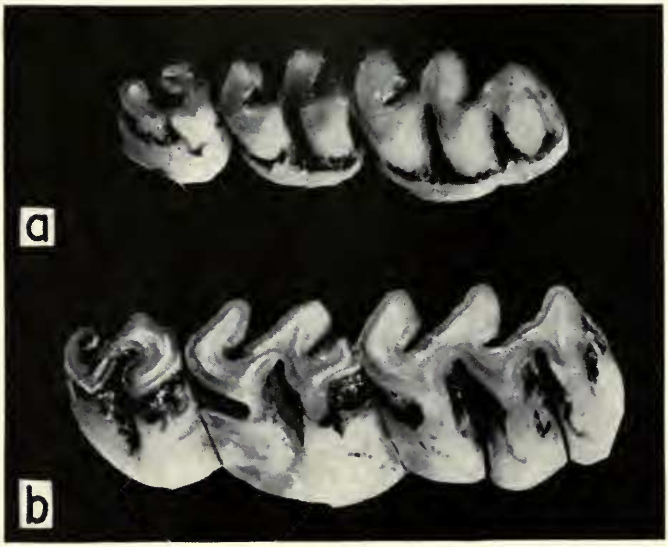

FIG. 114.—Right upper molars of *a*, *Phyllotis griseoflavus; b*, *Andinomys edax*. Note normal plane crown surfaces.

Comparisons

The inwardly flexed upper incisors with cutting edges forming a sharp angle distinguish *Andinomys* from all other phyllotines. The interfrontal fontanelles are larger and more consistently present in *Andinomys* than in other cricetines. External appearance of *Andinomys* is not striking. The animal compares with *Phyllotis griseoflavus* and *P. micropus* in size, but resembles the latter in color, texture of pelage and, except for its slightly broader hind feet, in limb proportions. Enamel pattern of upper molars of *Phyllotis griseoflavus* is essentially as in *Andinomys*; the teeth themselves, however, though high crowned are not prismatic, the cusps less sharply angulate, m_1 with procingulum simplified as contrasted with the advanced trilobate pattern of the same part of the tooth in *Andinomys*. Interfrontal fontanelles occur sporadically in a number of cricetines. They are common, though rarely well developed, in *Phyllotis micropus*, and nearly as prevalent in the sigmodont red-nosed vole *Neotomys* as in *Andinomys*. Also, in *Neotomys*, the high median ridge of the posterior portion of the palate, and the inwardly flexed incisors are as in *Andinomys*. The incisors of *Neotomys*, however, are grooved, their cutting edges straight or forming a very obtuse angle, the molars notably compressed antero-posteriorly, m^3 longer than wide, larger than m^2, and with second secondary and second minor folds present and well developed in adult. *Andinomys* is readily distinguished from *Neotomys* by these and any number of other external, cranial and dental characters. Molars of the phyllotine *Chinchillula* are as hypsodont and flat crowned as in *Andinomys* but their enamel pattern has been simplified to an 8-shaped figure in adult upper and lower second and third molars. The color pattern of *Chinchillula* is unique and cannot be confused with *Andinomys*.

The prismatic crowns and triangulate cusps of the molars of *Andinomys* recall those of the North American woodrat *Neotoma* (figs. 115, 116) but there are trenchant differences between the two genera in number and disposition of cusps and orientation of the folds. In *Neotoma*, apex of each of first and second primary folds of m^{1-2} extends well across crown and nearly, or quite, touches enamel wall of opposite side; in *Andinomys* only the first primary fold extends nearly to enamel of opposite side; first minor fold of m^{2-3}, absent in *Neotoma*, is present, though weakly defined in *Andinomys*; m^3 with three subequal lophs on outer side in *Neotoma* has but two subequal lophs in *Andinomys*; procingulum of m_1, never trilobate in *Neotoma*, is trilobate in juvenal *Andinomys*; outer main cusps of m_{1-2} one-half or less size of analogous cusps of inner side in *Neotoma* are subequal in *Andinomys*; in m_{1-2} of *Neotoma* apices of first primary and first minor folds touch, and apices of second primary and major folds touch while in *Andinomys* only apices of second primary and major folds nearly or quite touch, the first primary being reduced; in *Neotoma* m_3 is 8-shaped, in *Andinomys* roughly C-shaped. Molars of *Hodomys* are slightly less specialized than those of *Neotoma*, m_1 with anterolophid present in juvenal, m_3 S-shaped. The marked tendency toward lamination, especially in m^3, present in neotomyine

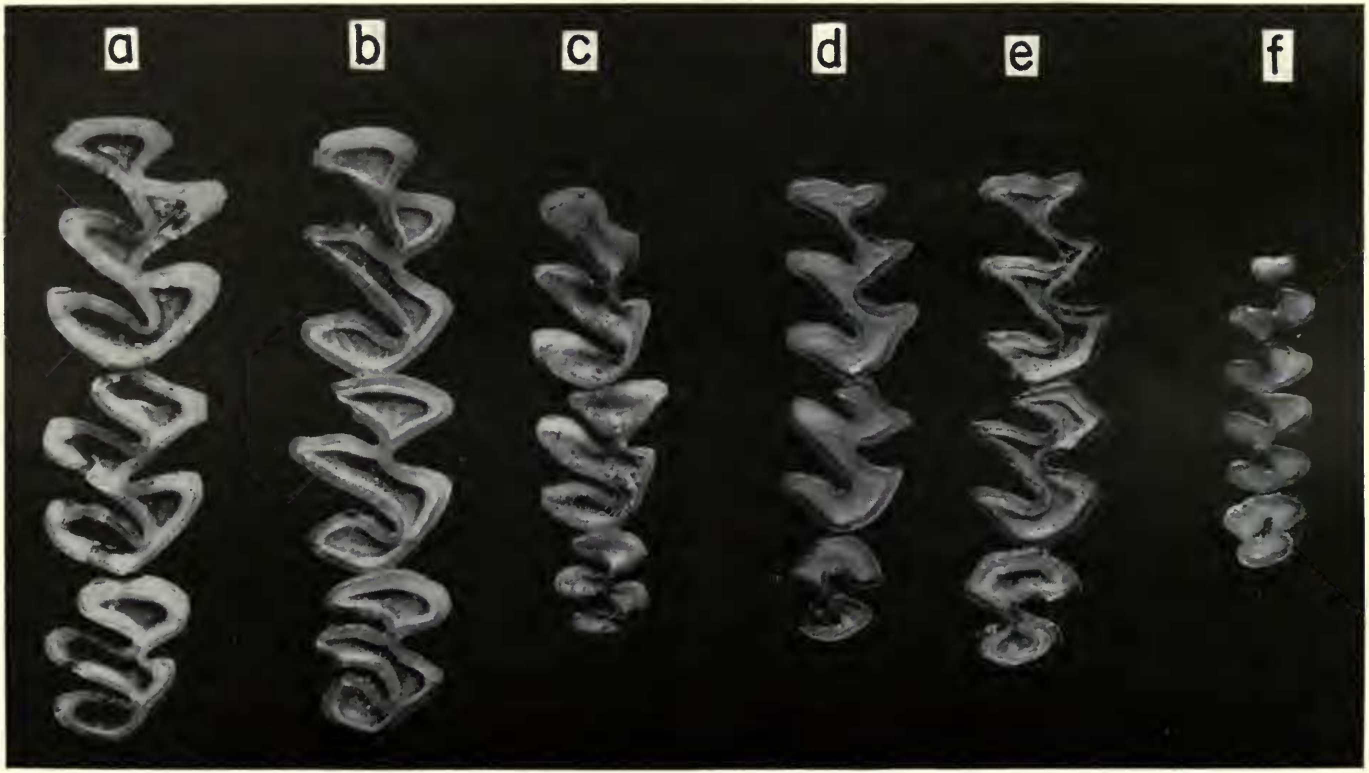

FIG. 115.—Right upper molars of *a*, *Neotoma* (*Hodomys*) *alleni*; *b*, *Neotoma* (*Teonoma*) *cinerea*; *c*, *Neotoma* (*Neotoma*) *mexicana*; *d*, *e*, *Andinomys edax*; *f*, *Phyllotis griseoflavus*. Note triangulation of cusps in all three genera.

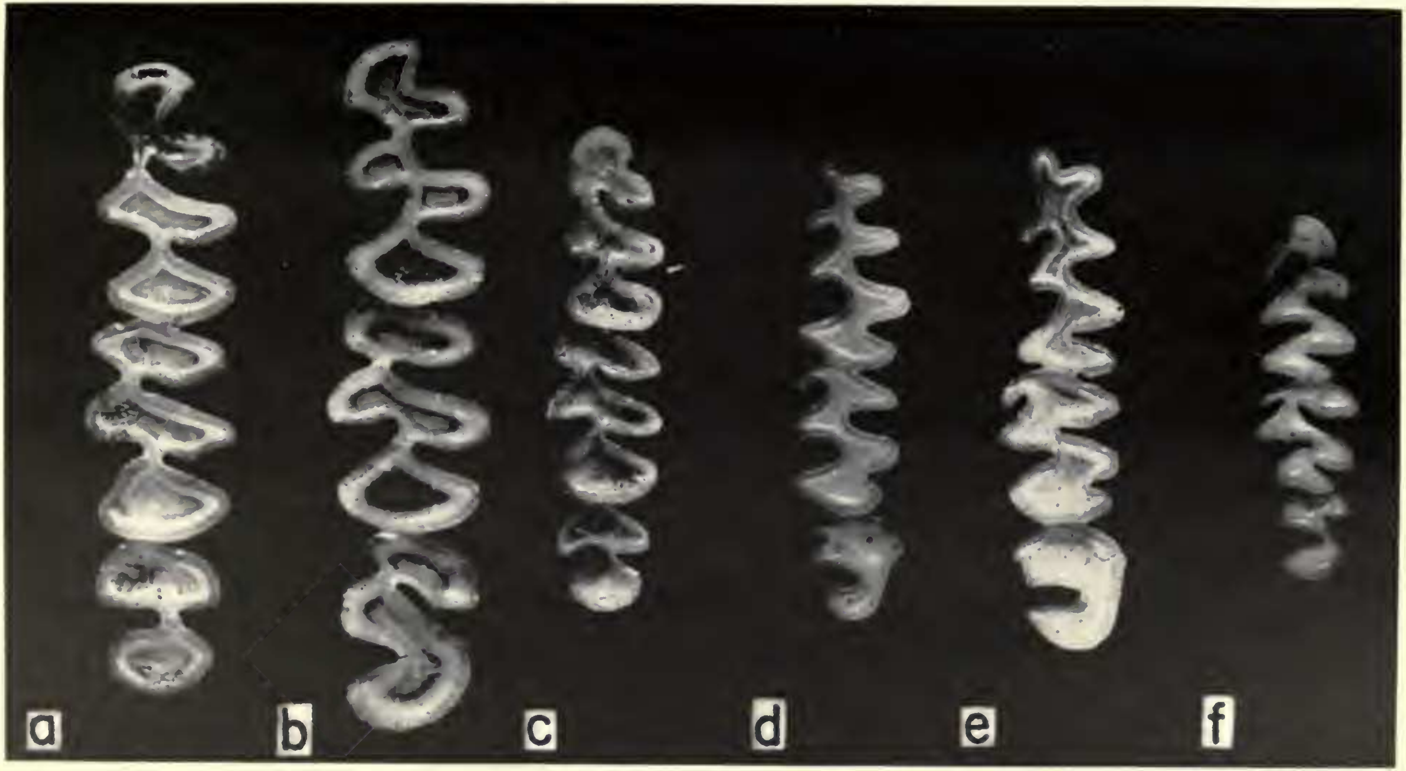

FIG. 116. Lower left molars of *a*, *Neotoma (Hodomys) alleni*; *b*, *Neotoma (Teonoma) cinerea*; *c*, *Neotoma (Neotoma) mexicana*; *d*, *e*, *Andinomys edax*; *f*, *Phyllotis griseoflavus*. Note triangulation of cusps.

rodents, is absent in *Andinomys*. Furthermore, no neotomyine shows incisors flexed inwardly as in *Andinomys*. Cranial characters distinguishing *Andinomys* from *Neotoma* are too obviously different to require analysis here. Gross differences in the structure of the glans penis and baculum are discussed elsewhere (cf. p. 20).

Variation

The lone species of the genus is pale in the Lake Titicaca region and becomes darker, as well as larger, southward into northwestern Argentina. A juvenal from Choro, Cochabamba, Bolivia, in the upper Amazonian drainage, is darker throughout than comparable individuals from other regions. Except for a narrowing of the braincase and interorbital region, the general proportions of the skull are not notably modified by increasing age; the interfrontal fontanelles are as prominent in old as in young individuals. Because of the high crowns, the enamel pattern of the molars varies widely with wear. Nevertheless, the diagnostic characters of the dentition are not obscured except in extremely worn teeth.

Taxonomy

Molars of *Andinomys*, and even more so those of *Chinchillula*, represent the extreme of hypsodonty in phyllotine rodents. Among long palate tetralophodont cricetines, hypsodonty with attendant prismatic shape of crown elements has gone even farther in the sigmodont coney rat, *Reithrodon*. A comparable evolution from bunobrachyodonty to columnar platyhypsodonty in cricetines with simple, or short, palates can be traced from *Haplomylomys* (ex *Peromyscus*) to its culmination in *Neotoma*.

The process of triangulation in *Andinomys* is repeated in several phyllotines, but in none are all triangular shaped elements closed. Triangulation is more advanced in neotomines and is extreme in microtines. In all forms considered the triangular outline of the dental elements appears in the unworn tooth but becomes progressively rounded during the course of wear.

Four extinct genera from the Pleistocene of eastern Argentina indicated by Osgood (1947, p. 173) as resembling *Andinomys* were described by Ameghino in 1889 (pp. 111–120). They are *Ptyssophorus* and *Tretomys*, both synonyms of *Reithrodon;* the third genus, *Bothriomys* is a *Euneomys*, and the fourth, *Necromys*, is the same as *Calomys*. Merriam (1894, p. 225) included the first two genera in his "subfamily" *Neotominae*.

Habits and Habitat

Andinomys lives in temperate zone puna, or *paramo*, and scrub country together with *Phyllotis darwini*. It is terrestrial, but may be scansorial as well. Emilio Budin, who collected most of the specimens recorded by Thomas, noted (*in* Thomas, 1913, p. 140) that *Andinomys* "lives in branches of trees where it makes its nest." It is very probable that Budín's field notes referred to another animal. There is nothing in the structure of *Andinomys*, and very little in its habitat, to indicate arboreal habits. Thirteen years later, Budín observed (*in* Thomas, 1926b, p. 603) that the rat "lives in round holes, quite clean, and the inside is carpeted with very fine straw; feeds on green herbs." Whether or not the burrow was of the rat's own making was not determined. During an intervening excursion, Budín (*in* Thomas, 1919d, p. 129) found the Chozchorito, the name he gave *Andinomys*, "among the rocks on the bank of a stream." The peculiar upper incisors of *Andinomys* indicate some special feeding or food-seizing habits (cf. p. 106).

Of three female *Andinomys* collected December 18, 1939, by Pearson (1951, p. 152) one contained three large embryos. Measurements given for the females, said to be adults, seem to be, rather, those of young individuals.

Andinomys edax edax Thomas

Andinomys edax Thomas, 1902, (6 March) Nature, **65**: 431. Thomas, 1902, (March), Ann. Mag. Nat. Hist., (7), **9**: 225—BOLIVIA: *Potosí* (El Cabrado, 3500 meters). Thomas, 1902, Proc. Zool. Soc. London, **1902**: 116, pl. 9, figs. 1–3 (skull), figs. 4–6 (molars). Thomas, 1913, op. cit., (8), **11**: 140—ARGENTINA: *Jujuy* (Maimará; Cerro de Lagunita; Maimará). Thomas, 1919, op. cit., (9), **4**: 129—ARGENTINA: *Jujuy* (Cerro Casabindo). Thomas, 1921, op. cit., (9), **8**: 611—ARGENTINA: *Jujuy* (Alfarcito; Sierra de Zenta). Thomas, 1926, op. cit., (9), **17**: 320—BOLIVIA: *Tarija* (Pinos; Sama). Thomas, 1926, op. cit., (9), **18**: 191—BOLIVIA: *Potosí* (Tupiza; Yuruma). Gyldenstolpe, 1932, K. Sv. Vet. Akad. Handl., **11**: 97, pl. 11, fig. 2 (skull of type), pl. 18, fig. 3 (upper molars of same).

Andinomys edax edax, Yepes, 1935, Anal. Mus. argentino Cienc. Nat., **38**: 342, fig. 1 (skull), figs. 2, 3*b*–*c* (molars), fig. 4*a* (tail)—ARGENTINA: *Jujuy* (Maimará; La Laguna; Sierra de Zenta). Yepes, 1938, Rev. Centro Estud. Doct. Cienc. Nat. Buenos Aires, **2**: 24—distribution. Sanborn, 1950, Mus. Hist. Nat. "Javier Prado," (A), Zool., no. 5: 10—PERU: *Puno* (Yunguyo). Pearson, 1951, Bull. Mus. Comp. Zool., **106**: 152—PERU: *Puno* (Juli, Lake Titicaca).

Type.—Old female, skin and skull, British Museum (Natural History) no. 2.2.2.15; collected 20 September, 1901, by Perry O. Simons.

Type locality.—El Cabrado, between Potosí and Sucre, Bolivia; altitude, 3700 meters above sea level.

Distribution (fig. 112).—From the Lake Titicaca region in Peru southward through the Bolivian highlands into the Andes and Sierras Pampeanas of Jujuy, northern Argentina and, probably, adjacent parts of the Argentine province of Salta; altitudinal range from 2000 to 5000 meters above sea level.

Characters.—Those of the genus; tail brown above, sharply defined white beneath.

Measurements.—See Table 63.

Specimens examined.—11. PERU.—*Puno:* 6 miles south of Yunguyo, 5 (CNHM). BOLIVIA.—*Potosí:* Estancia Yuruma, 2 (CNHM); *Cochabamba:* Choro, 1 (CNHM). ARGENTINA.—*Jujuy:* Mountains west of Yala, 3 (CNHM).

Andinomys edax lineicaudatus Yepes

Andinomys edax, Thomas, 1919, Ann. Mag. Nat. Hist., (9), **3**: 492—ARGENTINA: *Catamarca* (Otro Cerro, "Rioja"). Thomas, 1926, op. cit., (9), **17**: 603—ARGENTINA: *Tucumán* (Ñorco, Vipos).

Andinomys edax lineicaudatus Yepes, 1935, Anal. Mus. argentino. Cienc. Nat., **38**: 345, fig. 46 (tail)—ARGENTINA: *Tucumán* (Cerro San Javier; Aconquija; Sierra de Tafi Viejo). Yepes, 1938, Rev. Centro Estud. Doct. Cienc. Nat. Buenos Aires, **2**, (4): 24 (separate)—distribution.

Type.—Adult female, skin and skull, Museo Argentino de Ciencias Naturales, Buenos Aires, no. 26147; collected 17 August, 1926, by Emilio Budín.

Type locality.—Cerro San Javier, Tucumán, Argentina; altitude, 2000 meters above sea level.

Distribution (fig. 112).—Sierras Pampeanas of Tucumán and Catamarca (Otro Cerro, "Rioja," is in Catamarca); altitudinal range, 2000 to 3000 meters above sea level.

Characters.—Tail with brown midventral line.

Measurements.—See Table 64.

Specimens examined.—1. ARGENTINA.—Rio Vallecito, Catamarca, 1 (MACN).

TABLE 63. —Measurements of *Andinomys edax edax* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
PERU							
Yunguyo[1]	150	107	31	—	33.6	18.7	7.5
BOLIVIA							
Yuruma	153	132	29[2]	26	—	—	—
El Cabrado[3]	160	145	30	25	37	—	7
ARGENTINA							
Yala	182	—	32	—	36.6	20.8	7.1
Yala	172	135	32	—	35.4	19.5	7.8
Maimara[4]	172	134	28[5]	24	36	21	7.5
Maimara[4]	162	135	28[5]	27	—	—	—
Maimara[4]	155	160	28[5]	22	34	19	7.0

[1] Juvenal.

[2] Dry.

[3] Type, from original description.

[4] *Ex* Yepes (1935, An. Mus. Arg. Cienc. Nat., 38: 347).

[5] Without claw.

TABLE 64. Measurements of *Andinomys edax lineicaudatus* Yepes

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
San Javier[1]	171	130	30	25	37	20	8
San Javier[2]	156	144	31	26	33	18	8
Tafi Viejo[2]	176	146	34	26	38	20	7
Aconquija[2]	170	140	32	22	36	20	7
Vallecito	145	142	35[3]	23	34.5(*ca.*)	18.5	7.8

[1] Of type, from original description.

[2] Of paratypes, from original description.

[3] Dry.

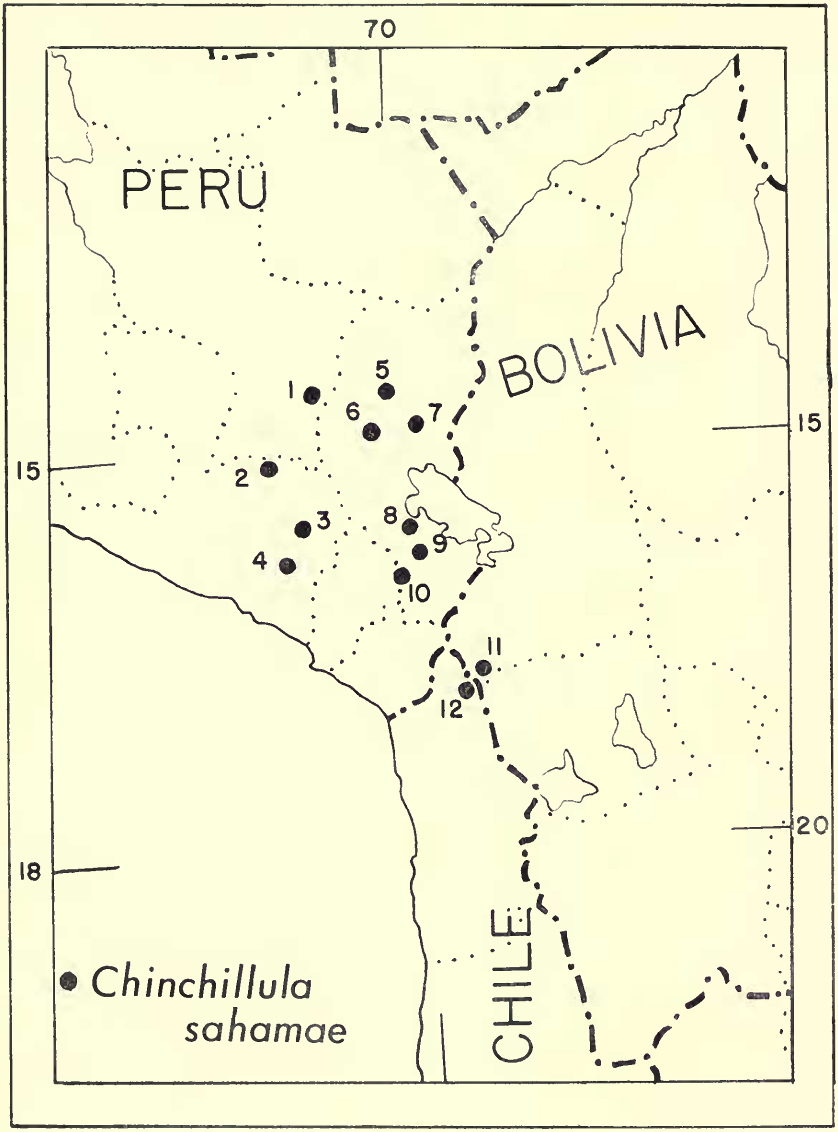
70
PERU
BOLIVIA
CHILE
15
15
18
20
1
2
3
4
5
6
7
8
9
10
11
12
● Chinchillula sahamae

FIG. 117.—Collecting localities of *Chinchillula sahamae*. See opposite page for explanation.

Genus **Chinchillula** Thomas

Chinchillula Thomas, 1898, Ann. Mag. Nat. Hist., (7), **1**: 280. Thomas, 1902, Proc. Zool. Soc. London, **1902**: 116, pl. 9, figs. 5, 7 (molars). Osgood, 1947, Jour. Mamm., **28**: 174.

Type species.—*Chinchillula sahamae* Thomas by original designation.

Included species.—*Chinchillula sahamae* Thomas.

Distribution

Figures 52, 117

From southern Cuzco, Puno and Arequipa departments in southern Peru, southward into Tarapacá, northern Chile and the departments of La Paz and Oruro, western Bolivia; altitudinal range, approximately 3500 to 5000 meters above sea level.

Characters

External.—Largest of the phyllotines and most distinctively colored New World cricetine; pelage long, silky, upper parts of body buffy to tawny overlaid with blackish mid-dorsally; upper half of sides like back, except for large white hip patch continuous with

EXPLANATION OF FIGURE 117

Chinchillula sahamae: Collecting localities and collectors.

Type locality in **boldface.**

PERU (1–10)

1. Cordillera de Sicuani, Cusco. I. Ceballos.
2. Cailloma, Arequipa. P. O. Simons; C. C. Sanborn and J. M. Schmidt at 14,500 feet.
3. Arequipa, Arequipa. P. O. Simons.
4. Sumbay, Arequipa. C. C. Sanborn at 13,500 feet.
5. Puerto Arturo, Puno. C. C. Sanborn.
6. Posoconi (Hacienda), Puno. C. C. Sanborn.
7. Picotani (Hacienda), Puno. C. C. Sanborn.
8. Collacachi (Hacienda), Puno. C. C. Sanborn.
9. Pairumani, Puno. O. P. Pearson at 13,000 feet.
10. Caccachara, Puno. O. P. Pearson at 16,000 feet.

BOLIVIA

11. **Esperanza, La Paz.** G. Garlapp at 4200 meters.

CHILE

12. Parinacota, Tarapacá. G. Mann.

white of lower half of sides and underparts; a dark brown lateral line often present between upper and lower halves of posterior portion of sides; dark brown to black patch on lower outer side of rump extended over outer side of thighs; inner sides of rump white, base of tail like back; white tips of guard hairs of rump and thighs projecting well beyond cover-hairs; brown of sides continuing over sides of arms; muzzle white; ears brown with white patch behind; large preauricular tufts white; fore and hind legs and feet white, digital tufts usually concealing the comparatively weak claws, plantar surface smooth, bare, the tubercles large; tail approximately one-half to three-fourths length of head and body combined, white with a brown mid-dorsal stripe or band, well haired and terminating in a thin pencil; mammae, $2-2=8$.

Cranial (figs. 61–63, 118, 119).—Dorsal surface of skull flattened, supraorbital region narrow, parallel-sided, the edges square or raised; temporal ridges obsolete or absent; nasals comparatively slender, except at flared anterior portion; interparietal well developed antero-posteriorly; zygomata well expanded, evenly bowed; fronto-parietal sutures meeting at midline to form a right or acute angle; distance across them on dorsal surface less than greatest width across fronto-maxillary sutures and less than alveolar length of molar row; anterior border of zygomatic plate sloped backward from below upward, and often with a slight tubercle on middle portion, upper anterior corner rounded; incisive foramina well opened; bony palate always extending well behind posterior plane of last molars; greatest width between inner borders of first molar equal to, or more than, greatest length of m^1; postero-lateral palatal depression shallow; mesopterygoid fossa broad, width at anterior base of pterygoid processes more than width of parapterygoid fossa measured at same plane; parapterygoid fossa deep in adults; bullae moderately inflated, less than length of molar row.

Dental (figs. 62, 63, 69, 119, 120).—Upper incisors long, orthodont or slightly opisthodont, anterior face smooth or, sometimes, weakly grooved; upper molar rows parallel-sided or slightly divergent posteriorly; upper first molar three-rooted, lower two-rooted; molars large, prismatic, crowns normally flat but sometimes secondarily terraced in old worn teeth; cusps subtriangular or subovate in outline; enamel pattern essentially 8-shaped; apices of opposing enamel folds never touching, each extending nearly to, rarely beyond, midline of molars; m^1 with procingulum subtriangular in adult, a subovate subcylindrical lamina in juvenal; postcingulum

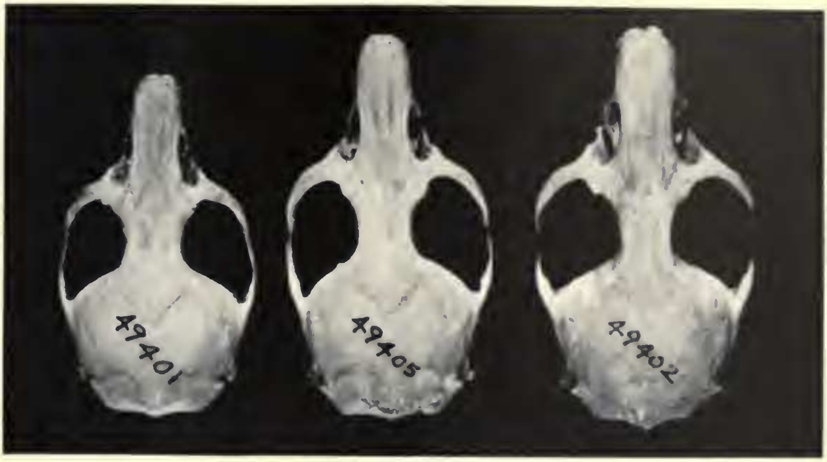

FIG. 118.—*Chinchillula sahamae.* Dorsal aspect of skulls, showing variation in size (less than × 1½).

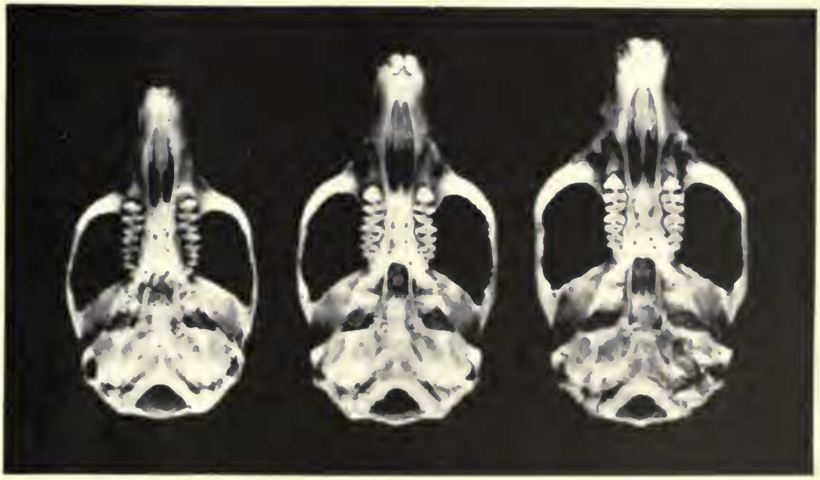

FIG. 119.—*Chinchillula sahamae.* Palatal aspect of skulls, showing variation in size (less than × 1½).

absent; m^{2-3} with pro- and postcingula absent, each molar with only a second primary and major fold; m_{1-3} without postcingula; procingulum of m_1 usually with an anterolingual stylid fused with a low, rudimentary anterolophid and nearly, or quite, isolating minor fold from outer margin of tooth; m_2 with minor fold indicated by a style-like anterolophid; first primary fold absent in m_{2-3}.

Comparisons

Among American cricetines, only the sympatric *Akodon jelskii pulcherrimus* shows some resemblance to *Chinchillula* in color pattern. The *Akodon* has similar white auricular tufts, sharply defined white lower halves of head, sides, rump, and dark outer sides of upper arms and thighs. It is, however, considerably smaller in size, with tail dark, nose reddish, and without black and white markings on posterior portion of body. The Eurasian hamster, *Cricetus*, offers some interesting points of resemblance to *Chinchillula* in its white auricular patches and pale sides of head and body. The unique arrangement of two white patches separated by the dark rump patch in *Chinchillula* is, in *Cricetus*, translated to the fore part of the body where two pale patches are separated by a dark gular band. The most remarkable resemblance in color, however, occurs in the unrelated North American kangaroo rats of the genus *Dipodomys*. Except for the absence of the dark rump patch in *Dipodomys*, the pattern is essentially the same in both genera. The skull of *Chinchillula* most nearly resembles that of *Andinomys*, but is larger throughout, nasals more tapered posteriorly, posterolateral palatal depressions not furrowed, mesopterygoid fossa wider, parapterygoid fossa deeper, interfrontal fontanelles absent, etc. Molars of *Chinchillula* are as hypsodont as in *Andinomys* but more simplified in enamel pattern than in any other phyllotine.

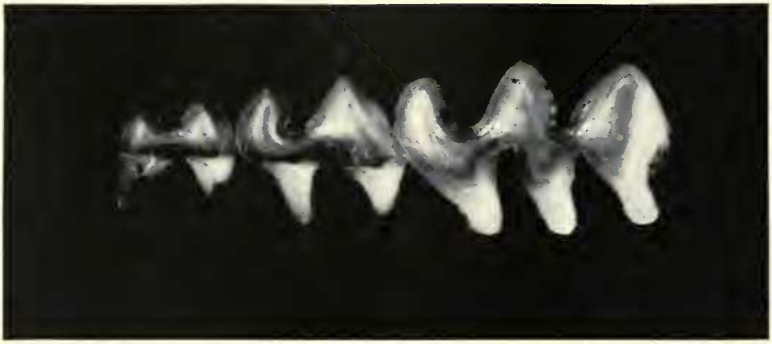

FIG. 120.—*Chinchillula sahamae*. Right upper molars, showing longitudinal sulcus and secondary terracing resulting from extreme wear.

Variation

The distinctive blackish and white markings of head, hips, rump and thighs are consistent, even in nestlings. There is some individual variation in ground color of back and upper half of sides, as well as in the intensity of the blackish overlay of back. Color and pelage of juvenals are precisely as in adults. Braincase and interorbital region are proportionately narrower in older than younger individuals. Faintly to moderately defined grooves on outer face of incisors are present in about 10 per cent of specimens examined. Molars of a juvenal with skull length 31.6, are unworn, the third just erupted. Larger specimens, including a juvenal with skull length 32.7, have fully functional and abraded molars.

The interparietal of a subadult (CNHM 49410) is paired, the median suture being complete, well defined and in line with the suture separating the parietals.

Taxonomy

Chinchillula is the best defined and most strikingly colored phyllotine. Its extreme specializations are large size, unique color pattern, angular fronto-parietal sutures, sloping anterior zygomatic plate and simplified enamel pattern of the molars. A tendency to specialization of the incisors is noted in the occasional presence of grooves; on the other hand, the hard palate and postpalatal fossae of *Chinchillula* are not greatly differentiated from the primitive phyllotine condition. Greater resemblance of *Chinchillula* to *Andinomys* in size, shape of skull and height of molars does not indicate a nearer relationship to it than to other phyllotines such as *Phyllotis boliviensis* and *P. micropus.* In external and dental characters *Chinchillula* and *Andinomys* are widely divergent.

Habits and Habitat

Field observations on *Chinchillula* of the Lake Titicaca region in southern Peru were made by Pearson (1951, p. 148). According to this authority, the rat lives in "rocky places at high altitudes. It is most often caught among boulders and along stone walls. The surrounding vegetation may be grass, tola, yareta, or many of the other plants common in the region. . . . It is nocturnal and herbivorous. At times, its enormous stomach is distended by more than 12 grams of green, finely ground, vegetable matter.

"*Chinchillula* is one of the rats known and distinguished by the natives, not so much because of its striking color pattern, but because its exceedingly deep and fine fur makes it valuable commercially. The skins are used as trim, or made into robes containing more than 150 skins. I never heard of a person who could be considered a professional *Chinchillula* trapper, but the skins were being sold by the natives at Santa Rosa [Puno] and Juli [Puno] for about 20 centavos apiece—the cost of a half-pound of rice. . . ."

The Chilean naturalist, Guillermo Mann (1945, p. 87) discovered *Chinchillula* in the puna zone of the northern Chilean province of Tarapacá. He expressed concern that persecution of the rodent for its fine pelt might lead to extermination of the species.

The pelage of other cricetines of the altiplano of Peru, Bolivia and the temperate zones of Argentina and Chile is as fine as, or finer than, that of *Chinchillula*. However, the larger size of the latter and, possibly, the greater ease with which it may be captured, may make its pelt a more profitable item of commerce.

Chinchillula sahamae Thomas

Chinchillula sahamae Thomas, 1898, Ann. Mag. Nat. Hist., (7), **1**: 280. Thomas, 1900, op. cit., (7), **6**: 469—PERU: *Arequipa* (Cailloma; Arequipa). Thomas, 1902, Proc. Zool. Soc. London, **1902**: 117, pl. 9, figs. 5, 7 (molars)—PERU: *Arequipa* (Cailloma; Arequipa). Mann, 1945, Biológica, Trab. Inst. Biol. Univ. Chile, fasc. 2: 87, figs. 39–41 (alimentary tract), pl. 33, fig. *b* (skin), pl. 34 (skull)—CHILE: *Tarapacá* (Parinacota). Sanborn, 1950, Mus. Hist. Nat. "Javier Prado," (A), Zool., no. 5: 10—PERU: *Arequipa* (Sumbay; Cailloma); *Puno* (Hacienda Collacachi; Hacienda Posoconi; Hacienda Picotani; Puerto Arturo). Mann, 1950, Invest. Zool. Chilenas, **1**, no. 2: 5—CHILE: *Tarapacá*. Pearson, 1951, Bull. Mus. Comp. Zool., **106**: 148—PERU: *Puno* (Caccachara; Pairumani).

Type.—Juvenal male, skin and skull, British Museum (Natural History) 98.3.16.6; collected June 25, 1897, by Gustav Garlepp. In the original description, the type was said to be "slightly immature." Measurements indicate it to be a nestling (cf. Thomas, 1902, Proc. Zool. Soc. London, p. 116, footnote).

Type locality.—Esperanza, about 50 kilometers north of Mt. Sajama, Pacajes, southwestern La Paz, Bolivia; altitude, 4200 meters above sea level.

Distribution (fig. 117).—As for the genus. The locality records for Bolivia and Chile are in the Lakes Titicaca–Poopo drainage basin. Pearson (supra cit.) includes "northern Argentina" in the range, but I find no published locality record for this country.

Characters.—Those of the genus.

Measurements.—See Table 65.

Specimens examined.—35, all in Chicago Natural History Museum. PERU.—*Cusco:* Cordillera de Sicuani, 1; *Puno:* Collacachi, 4; Picotani, 9; Posoconi, 2; Puerto Arturo, 1; *Arequipa:* Cailloma, 15; Sumbay, 3.

TABLE 65. Measurements of *Chinchillula sahamae* Thomas

Locality	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
PERU							
Cailloma[1]	163(148-182)10	105(98-118)10	34.5(33-36)10	36(34-38)10	37.2(35.6-38.9)9	20.4(19.3-21.4)9	7.5(7.0-7.9)9
Sumbay	157	99	33	—	38.6	20.9	7.7
Picotani	154	96	35	—	35.9	20.5	7.7
"	177	98	35	—	38.6	21.5	7.7
"	173	109	36	—	38.9	21.1	7.5
"	176	106	35	—	39.9	22.5	6.9
"	188	92	35	—	40.1	22.6	7.1
"	181	104	36	—	—	21.0	7.1
Posoconi	165	113	35	—	38.3	20.9	7.7
Collacachi	165	90	34	—	36.0	20.2	7.7
"	156	94	33	—	36.2	19.5	7.7
BOLIVIA							
Esperanza[2]	122	59	28	23	—	16.5	7.2

[1] Includes subadults.

[2] Type, from original description; basal length of skull, approximately 25 mm.

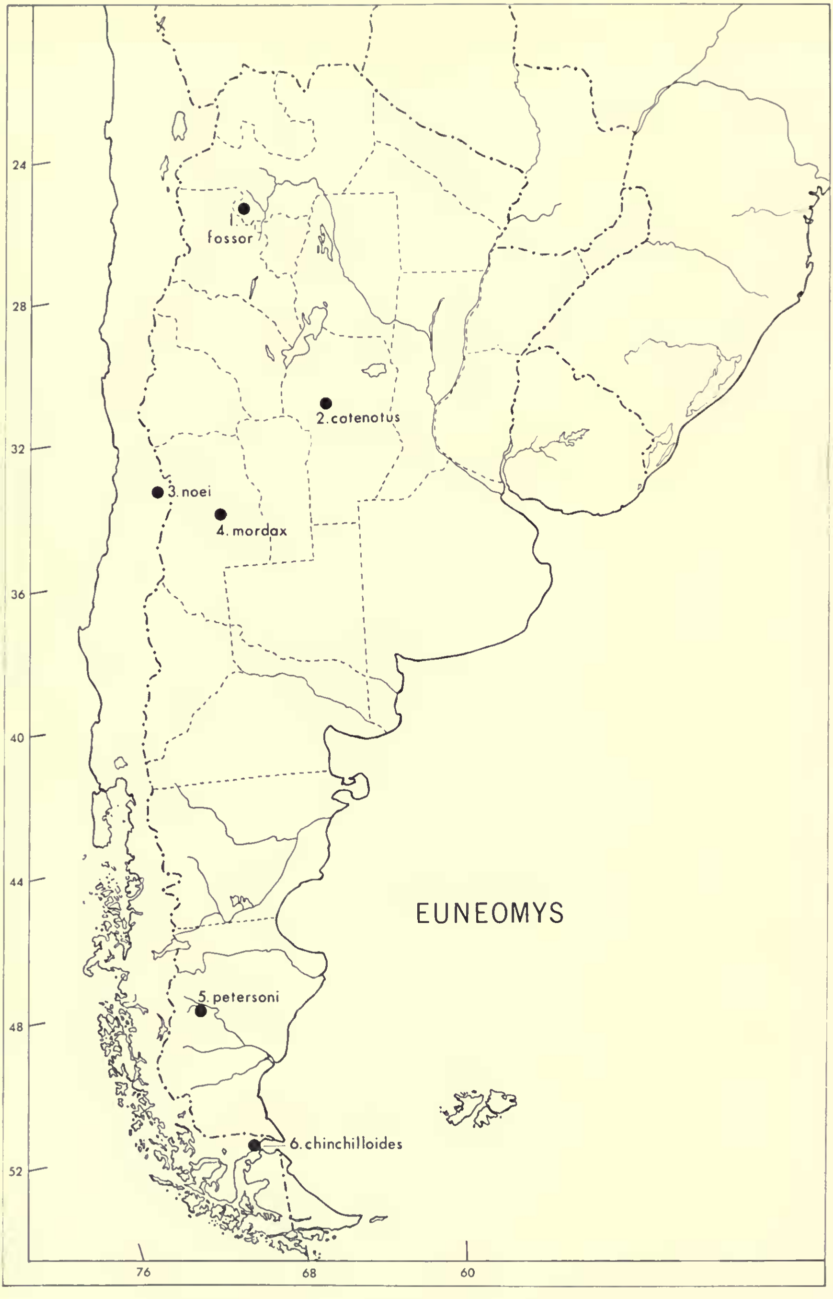
24
28
32
36
40
44
48
52
76
68
60
1. fossor
2. cotenotus
3. noei
4. mordax
5. petersoni
6. chinchilloides
EUNEOMYS

FIG. 121.—Type localities of nominal species and subspecies of *Euneomys chinchilloides.*

Genus **EUNEOMYS** Coues

Reithrodon, Waterhouse, 1839, Zool. Voy. "Beagle," p. 68—part, *R. chinchilloides* Waterhouse, only.

Euneomys Coues, 1874, Proc. Acad. Sci. Philadelphia, **26**: 185—subgenus of *Reithrodon;* type by monotypy, *R. chinchilloides* Waterhouse. Coues, 1877, Monogr. N. A. Rodents, pp. 118, 119. Thomas, 1901, Ann. Mag. Nat. Hist., (7), **8**: 254—genus. J. A. Allen, 1903, Bull. Amer. Mus. Nat. Hist., **19**: 194—taxonomic history. J. A. Allen, 1905, Princeton Univ. Exped. Patagonia, **3**, (1): 66—taxonomic history. Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 142—characters; classification.

Bothriomys Ameghino, 1889, Act. Acad. Nac. Cienc. Rep. Argentina, **6**: 118—type, *B. catenatus* Ameghino (Pleistocene).

[?]*Chelemyscus* Thomas, 1925, Ann. Mag. Nat. Hist., (9), **15**: 584–585—type, *Reithrodon fossor* Thomas.

Type species.—*Reithrodon chinchilloides* Waterhouse.

Included species.—*Euneomys chinchilloides* Waterhouse, *E. noei* Mann, *E. mordax* Thomas, *E. catenatus* Ameghino, *E. fossor* Thomas.

Distribution

Figure 121

Andes of Chile and Argentina from approximately 33° south latitude to Cape Horn.

EXPLANATION OF FIGURE 121

Type localities of species and subspecies of *Euneomys*.

Euneomys fossor Thomas

1. "Salta Province, N. Argentina." Precise locality is unknown but arbitrarily shown in southwestern Salta. It is doubtful if the range of *Euneomys* extends into this province.

Euneomys catenatus Ameghino

2. Córdoba, Córdoba, Argentina. The type and only specimen is a Pleistocene fossil. Living representatives of *Euneomys* are not known to occur in Córdoba Province.

Euneomys noei Mann

3. Valle de la Junta, Canyon of the Río Volcán, Santiago, Chile.

Euneomys mordax Thomas

4. San Rafael, Mendoza, Argentina.

Euneomys chinchilloides petersoni J. A. Allen

5. Upper Río Chico, near the Cordilleras, Santa Cruz, Argentina.

Euneomys chinchilloides chinchilloides Waterhouse

6. Straits of Magellan, near eastern entrance, Tierra del Fuego, Chile.

Characters

External.—Size large, body heavy, vole-like, tail from 40 to 70 per cent of head and body length, brown above, white beneath, thinly haired, without well defined terminal tuft; ears moderate; hind foot broad, white above, fifth hind toe, less claw, extending to base of second phalanx of fourth toe, first hind toe to slightly beyond base of second; heel thickly haired, plantar surface of sole bare, lightly scutulated, with 6 well developed pads, claws weak; pelage thick, lax, the hairs crinkled; upper parts of body mixed buff and black, gray underparts not sharply defined, washed with buff; an ochraceous lateral line sometimes present.

Cranial (figs. 61–63, 122).—Dorsal contour of skull convex; supraorbital region narrow, parallel-sided, the edges square or raised, never beaded; interparietal well developed; zygomatic arches broadly expanded posteriorly, greatest width across them more than distance from posterior tips of nasals to anterior border of supraoccipital; anterior edge of outer zygomatic plate straight, the upper corner rounded; portion of maxillo-premaxillary suture below antorbital foramen directed forward in a line approximately parallel to longitudinal plane of palate; incisive foramina narrow, pointed posteriorly and extending behind anterior plane of first molars; posterior half of palate marked by a pair of large pitted depressions; mesopterygoid fossa one-half or less width of parapterygoid fossa, measured at same plane; parapterygoid fossa moderately deep, subrectangular in outline, anterior wall sloped, not undercut; outer side of mandible with capsular projection strongly pronounced at base of coronoid process.

Dental (figs. 62, 63, 69, 123).—Upper incisors opisthodont, their anterior faces marked by a well defined groove near midline; upper molar rows slightly divergent posteriorly; upper first molar 3-rooted, lower 2-rooted; crowns high, their occlusal surface plane, cusps lozenge-shaped, the intervening enamel folds greatly compressed anteroposteriorly; enamel pattern of each worn upper and lower second and third molars distinctly S-shaped; procingulum of $m_{\overline{1}}$ cylindrical in form, its occlusal surface cordate in outline and isolated from protoconid and metaconid, except in extremely worn tooth, by confluence of minor and first secondary folds; first primary fold of $m^{\underline{2-3}}$ reduced in juvenal, obsolete or absent in adult; postcingulum of upper molars vestigial, the second secondary fold reduced to a small enamel island in juvenals and persistent only in young adult $m^{\underline{3}}$; minor folds absent in $m\frac{2-3}{2-3}$; procingula of $m_{\overline{2-3}}$ obsolete; second primary fold

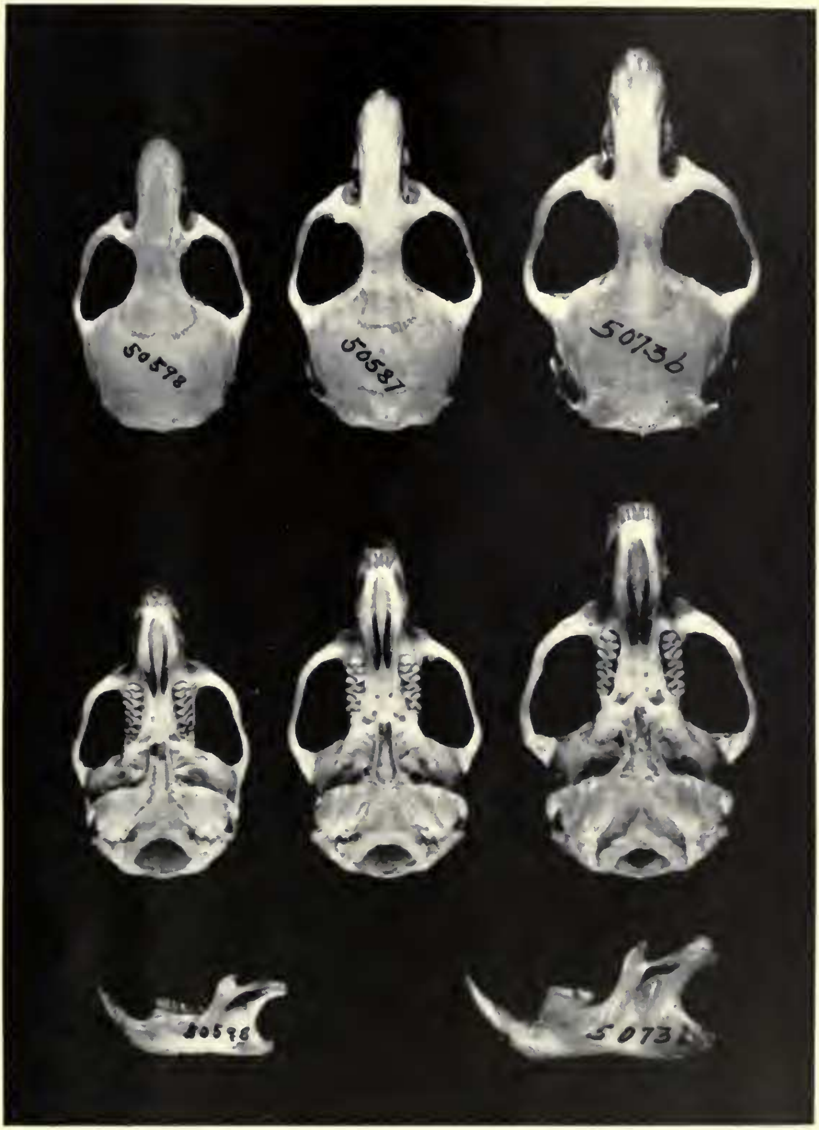
50598
50587
50736
50598
50731

FIG. 122.—*Euneomys chinchilloides.* Dorsal and ventral aspects of skulls, and mandibles, showing variation in size (about × 1½).

of $m_{\overline{2}}$ present in all but old adults, of $m_{\overline{3}}$ indicated only in unworn tooth; anterolabial stylid usually present and well developed.

Comparisons

In color and bulk of body, *Euneomys* resembles *Andinomys* and *Phyllotis micropus*, but the tail of the first is much shorter. Cranially, there is some resemblance to *Phyllotis pictus*, but the dorsal contour of the skull of *Euneomys* is more convex, though not arched as in *Galenomys*. Characters distinguishing *Euneomys* from all phyllotines include the nearly horizontal portion of the maxillo-premaxillary suture below the infraorbital foramen, antero-posterior compression of the enamel folds of the molars, lozenge-shaped cusps and procingulum, laminate and cylindrical procingulum of $m_{\overline{1}}$, distinct S-shaped pattern of moderately worn crowns of upper and lower second and third molars, and deeply grooved upper incisors. Involution of molars into a sigmoid pattern has gone farther in *Euneomys* than in true sigmodont rodents (*Sigmodon*, *Holochilus*, *Reithrodon*, *Neotomys*). In the latter, the pure sigmodont pattern is clearly defined only in $m_{\overline{3}}$. *Euneomys* is further separated from sigmodonts by less specialized hind feet, unmodified anterior border of zygomatic plate, comparatively shallow parapterygoid fossa, and the highly modified procingulum of $m_{\overline{1}}$. The procingulum of $m_{\overline{1}}$ in *Sigmodon* also tends to lamination, and in the newly erupted tooth of some individuals may be laminate, but its outline is triangular and an anterior median fold is lacking.

Taxonomy

Euneomys is closely related to both phyllotine and sigmodont rodents without being a member of either group. The rat is a highly specialized form that retains many phyllotine characters, but goes far beyond all other cricetines in development of the sigmoid pattern in virtually all molars. The cylindrical, laminate procingulum of the first lower molar of *Euneomys* is also unique among cricetines. Inclusion of a revision of the genus in this monograph is justified by historical relationships, and the probability that students may, with reason, look for it here.

The mandible and lower molars of *Bothriomys catenatus* Ameghino (1889, atlas, pl. 4, fig. 13,*d*) show all essential characters of *Euneomys chinchilloides*. Discrepancies between the figured molars of *Bothriomys* and molars of Recent cricetines with which comparisons have been made are certainly attributable to artistic liberties.

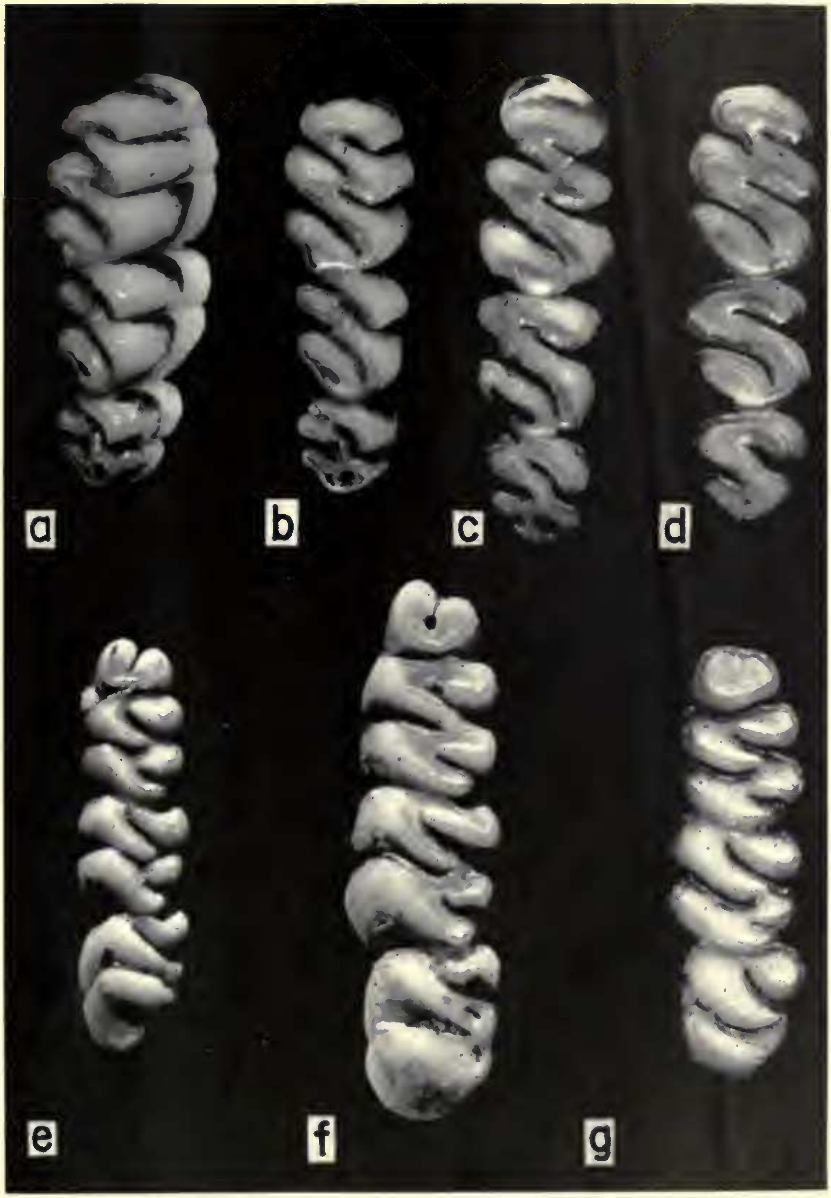

FIG. 123. *Euneomys chinchilloides*, right upper and left lower molars. *a*, unworn uppers, oblique view; *b*, same, nearly full crown view; *e*, lowers of same; *c*, *f*, juvenal; *d*, *g*, adult.

Resemblances between *Bothriomys* and *Andinomys* noted by Osgood (1947, p. 173) are of a superficial order.

The genus *Chelemyscus* was erected by Thomas to contain *Reithrodon fossor* Thomas. The type species is known from only a single specimen represented by a skin indistinguishable from that of *Notiomys macronyx* and a skull like that of a *Euneomys chinchilloides*. The possibility that the type might be a composite of an improperly associated skin and skull was suggested by Thomas in the following footnote to the original description (1899, p. 281). "The skull should be taken as the type if it were hereafter shown not to belong to the skin; but it was extracted in the Museum on arrival, so that any mistake seems quite impossible." Osgood (1943, p. 164), however, took exception. "Such mistakes," he declared, "are quite possible, as has been shown in other cases and, in view of the failure of collectors to obtain the species again during the past thirty years of activity, it seems more than probable that the type of *fossor* is composite, the skin being *Notiomys* and the skull *Euneomys*. The type is an old specimen 'presented by the La Plata Museum through Dr. F. P. Moreno' and said to have proceeded from Salta Province, Argentina, without exact locality. It is perhaps ungracious to discredit it without actual examination of the specimen, but the general evidence seems very much against it. The genus *Chelemyscus*, which is based exclusively upon it, has no characters except those that might be the result of a transposed skull; that is, *Chelemyscus* has no characters of its own, its external characters being strictly those of *Notiomys* and its cranial characters those of *Euneomys*. Unless additional specimens are forthcoming, therefore, this genus is suspect and deserves no better position than in a 'hypothetical' list."

Cabrera (1961, pp. 499–500), without allusion to its clouded status, recognized *Chelemyscus* as a valid subgenus of *Euneomys*. He gave no indication of having examined the type species or any bona fide specimen of the taxon.

Pending further investigation, *Chelemyscus* is here treated as an absolute synonym of *Euneomys* on the basis of published descriptions of its cranial and dental characters.

Nominal Species and Subspecies

Euneomys chinchilloides chinchilloides Waterhouse

Reithrodon chinchilloides Waterhouse, 1839, Zool. Voy. "Beagle," p. 72, pl. 27 (animal), pl. 34, fig. 20 (skull, molars). Gay, 1847, Hist. Chile, Zool., **1**: 120. Burmeister, 1879, Descr. Phys. Rep. Argentina, **3**: 231. Thomas, 1891, in Milne Edwards, Miss. Scient. Cap, vol. 6, Mamm., p. A 29, pl. 3, fig. 2 (animal)—CHILE: *Magallanes* (Orange Bay, Cape Horn).

R[eithrodon] chinchilloides, Thomas, 1881, Proc. Zool. Soc. London, **1880**: 696—comparison; measurements.

Reithrodon (Euneomys) chinchilloides, Coues, 1877, Monogr. N. A. Rodents, **1**: 119—characters.

E[uneomys] chinchilloides, Thomas, 1901, Ann. Mag. Nat. Hist., (7), **8**: 254—classification.

Euneomys chinchilloides, J. A. Allen, 1905, Princeton Univ. Exped. Patag., **3**, (1): 67. Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 142—classification.

Euneomys chinchilloides chinchilloides, Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 214, fig. 31 (skull)—characters; distribution.

Euneomys ultimus Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 185—type locality, St. Martin's Cove, Hermite Island, Cape Horn Islands, Tierra del Fuego, Chile.

Euneomys chinchilloides ultimus, Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 216—classification.

Type.—Juvenal, British Museum (Natural History), no. 55.12.26.111; collected by Charles Darwin. The type was originally "preserved in spirits, and has since been mounted."

Type locality.—Straits of Magellan, near eastern entrance, Tierra del Fuego, Chile.

Euneomys chinchilloides petersoni J. A. Allen

Euneomys petersoni J. A. Allen, 1903, Bull. Amer. Mus. Nat. Hist., **19**: 192. J. A. Allen, 1905, Princeton Univ. Exped. Patagonia, **3**, (1): 68, pl. 13, fig. 4 (skull), pl. 14, figs. 6-7 (molars)—ARGENTINA: *Santa Cruz* (upper Río Chico). Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 216—synonymy; distribution.

Euneomys dabbenei Thomas, 1919, Ann. Mag. Nat. Hist., (9), **4**: 127—ARGENTINA: *Santa Cruz* (type locality, Lago Viedma).

Type.—Adult female, skin and skull, U. S. National Museum, no. 84198; collected February 10, 1897, by O. A. Peterson.

Type locality.—Upper Río Chico, near the Cordilleras, Santa Cruz, Argentina.

Euneomys noei Mann

Euneomys noei Mann, 1944, Biológica, Univ. Chile, fasc. 1: 95, fig. 1 (skull), fig. 2 (carpalia), pl. 1 (skin), pls. 2, 3 (skulls), pl. 4 (molars), pl. 5 (skeleton), pl. 6 (embryo), pl. 7 (limb bones), pl. 8 (digestive tract).

Type.—Male, skin and skull, Guillermo Mann Collection no. 179-II; collected 29 February, 1944, by Guillermo Mann.

Type locality.—Valle de la Junta, Canyon of the Río Volcán, Santiago, Chile; altitude, 2,400 meters.

Remarks.—Doubtfully separable from *Euneomys mordax* Thomas.

Euneomys mordax Thomas

Euneomys mordax Thomas, 1912, Ann. Mag. Nat. Hist., (8), **10**: 410.

Type.—Adult female, skin and skull, British Museum (Natural History), no. 55.12.24.199; collected by Thomas Bridges.

Type locality.—San Rafael, Mendoza, Argentina.

Remarks.—Regarded by Cabrera (1961, p. 500) as a species of the dubious *Chelemyscus.* There is a greater probability that *mordax* may prove to be no more than a subspecies of *Euneomys chinchilloides.*

Euneomys catenatus Ameghino

Bothriomys catenatus Ameghino, 1889, Act. Acad. Nac. Cienc. Rep. Argentina, **6**: 118, atlas, pl. 4, figs. 13–13*c* (mandible), fig. 13*d* (lower molars).

Type.—Left mandible with complete dentition.

Type locality.—Vicinity of Córdoba, Córdoba, Argentina, "Piso bonaerense de la formacion pampeana (plióceno superior)," now regarded as Pleistocene.

?Euneomys fossor Thomas

Reithrodon fossor Thomas, 1899, Ann. Mag. Nat. Hist., (7), **4**: 280.

[*Euneomys*] *fossor*, Thomas, 1916, Ann. Mag. Nat. Hist., (8), **17**: 143—classification.

[*Chelemyscus*] *fossor*, Thomas, 1925, Ann. Mag. Nat. Hist., (9), **15**: 585—type of genus.

"*Reithrodon*" *fossor*, Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30**: 164—type skin a *Notiomys macronyx*, type skull a *Euneomys.*

Euneomys fossor, Cabrera, 1961, Rev. Mus. argentino Cienc. Nat. "Bernardino Rivadavia," **4**: 500.

Type.—Skin and skull, British Museum (Natural History) no. 99.2.22.25; presented by the Museo de La Plata, Argentina, through Dr. F. P. Moreno; "the skull should be taken as type if it were hereafter shown not to belong to the skin" (Thomas, 1899, footnote, p. 281).

Type locality.—"Salta Province," Argentina.

Remarks.—Present allocation of "*Reithrodon*" *fossor* to *Euneomys* is based on cranial and dental characters only, as suggested by

Thomas in the original description. Regarding external characters, Thomas (op. cit., p. 282) states that the "resemblance to *A[kodon,* i.e., *Notiomys*] *macronyx,* inhabiting the same districts, amounts practically to identity, there being absolutely no single character, of size, proportions, or colour, which would make the keenest-eyed 'splitter' suppose that the skin of *R. fossor* did not belong to *Akodon* [=*Notiomys*]."

Contrary to the belief expressed by Thomas, the supposed type locality of "*Reithrodon*" *fossor,* in Salta Province, Argentina, lies at least 500 miles north of the nearest locality record for living representatives of either *Notiomys* or *Euneomys.*

TABLE 66.—Measurements of the Nominal Forms of *Euneomys*[1]

(Measurements are from the original descriptions of the type specimens unless otherwise indicated)

Name	Sex	Head and body	Tail	Hind foot	Ear	Skull, greatest length	Zygomatic breadth	Alveolar length of molar row
chinchilloides	—	127	59	25.4	12[2]	29.6	18.0	5.8[7]
chinchilloides[3]	♂♂	156,127,123	81,73,69	32,30,31	—	34.7,31.6,30.1	21.0,18.8,18.4	6.4,6.3,6.2
dabbenei	♂	90	53	24	14[2]	25.2	15.6	5.3[7]
fossor	—	119	53	25	—	35.0	20.5	6.5
mordax	♀	147[4]	78	28	—	31	20	6.1
noei	♂	130	85	32	24	32	18.5	6.0
petersoni	♀	115	60	26	—	30.5	17.5	5.2[7]
petersoni[5]	♀, ♂	138,135	63,58	27,29	—	30.9,30.1	18.7,18.1	5.9,6.0
ultimus	♂	129	90	30	19	33.0[6]	20.3[6]	6.0

[1] Measurements of the extinct *Bothriomys catenatus* Ameghino, known from a mandible only, include $m_{\overline{1-3}}$, 5 mm.; diastema, 4 mm.

[2] From crown.

[3] CNHM 50736 from Lago Fagñano, Tierra del Fuego, Argentina; CNHM 50601, 50600, both subadults, from Punta Arenas, Chile.

[4] External measurements from dry skin, "no doubt stretched."

[5] CNHM 50597, 50592.

[6] Of adult specimen in Paris Museum *ex* Thomas (1912, p. 410).

[7] Crown length.

Literature Cited

Allen, J. A.

1891. Notes on new or little known North American mammals, based on recent additions to the collections of mammals in the American Museum of Natural History. Bull. Amer. Mus. Nat. Hist., **3**: 263–310.

1905. Mammalia of southern Patagonia. Reports of the Princeton University Expeditions to Patagonia, 1896–1899, **3**, Zoology, pt. 1: 210 pp., 29 pls.

Ameghino, F.

1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. Act. Acad. Nac. Cienc. Rep. Argentina, Córdoba, **6**: xxxii+1027 pp. and atlas.

Anderson, Sydney

1960. The baculum in microtine rodents. Univ. Kansas Publ., Mus. Nat. Hist., **12**, (3): 181–216, 49 figs.

Azara, F.

1801. Essais sur l'histoire naturelle des quadrupèdes de la province du Paraguay. **2**: 499 pp. Paris.

1802. Apuntamientos para la historia natural de los quadrúpedos del Paraguay y Río de la Plata. **2**: i–iii+328 pp. Madrid.

Bader, Robert S.

1959. Dental patterns in *Peromyscus* of Florida. Jour. Mammal., **40**: 600–602, 1 table.

Baird, Spencer F.

1859. Mammals of North America. pp. i–xxxiv+764, 87 pls. Philadelphia.

Barrera, J. M., de la

1936. Peste rural. Rev. Inst. Bacteriológico, Buenos Aires, **7**: 439–506.

1939. Contribución al conocimiento de la peste selvática en la Argentina caracteres del brote de Mendoza en 1937. Rev. Inst. Bacteriológico, Buenos Aires, **8**: 423–454.

1940. Estudios sobre peste selvática en Mendoza. Rev. Inst. Bacteriológico, Buenos Aires, **9**: 565–586.

Biggers, J. D., M. R. Ashoub, Anne McLaren, and Donald Michie

1958. The growth and development of mice in three climatic environments. Jour. Experiment. Biol., **35**: 144–155.

Birabén, M., and M. I. Birabén

1937. Viaje alrededor de Santa Cruz. Rev. Mus. La Plata, (n.s.), sec. oficial, **1936**, pp. 93–164, 31 figs.

Blair, W. Frank

1948. Population density, life span, and mortality rates of small mammals in the blue-grass meadow and blue-grass associations of southern Michigan. Amer. Midl. Nat., **40**: 395–419.

BROWN, W. L., JR., and E. O. WILSON

1956. Character displacement. Syst. Zool., **5:** 49–64, 6 figs.

BURMEISTER, H.

1854. Systematische Uebersicht der Thiere Brasiliens. Säugethiere, Berlin, pp. i–x+342.

BURT, WILLIAM HENRY

1960. Bacula of North American mammals. Univ. Michigan Mus. Zool., Misc. Publ. no. 113: 76 pp., 15 pls.

BUTTERWORTH, BERNARD B.

1960. The cricetid mouse, *Calomys*, from Venezuela. Jour. Mammal., **41:** 517–518.

CABRERA, A. L.

1953. Esquema fitogeográfico de la república Argentina. Rev. Mus. La Plata, (n.s.), 8, Botánica, pp. 87–168, 12 figs.

1961. Catálogo de los mamíferos de America del Sur. Rev. Mus. argentino Cienc. Nat. "Bernardino Rivadavia," **4**, (2): 309–732.

CALHOUN, J. B.

1949. The study of wild animals under controlled conditions. Ann. New York Acad. Sci., **51:** 113–122.

CLARK, FRANK H.

1938. Inheritance of pectoral buff spotting in the cactus mouse, *Peromyscus eremicus*. Jour. Heredity, **29:** 79–80.

CONSTANTINE, DENNY G.

1957. Color variation and molt in *Tadarida brasiliensis* and *Myotis velatus*. Jour. Mammal., **38:** 461–466.

1958. Bleaching of hair pigment in bats by the atmosphere in caves. Jour. Mammal., **39:** 513–520.

COSTA LIMA, A. DA, and C. R. HATHAWAY

1946. Pulgas. Bibliografía, catálogo e hospedadores. Mem. Inst. Oswaldo Cruz, **4:** 522 pp.

COUES, E.

1874. Synopsis of the Muridae of North America. Proc. Phila. Acad. Nat. Sci., pp. 173–196.

CRESPO, JORGE A.

1944. Relaciones entre estados climáticos y la evolución de algunos roedores de campo. Rev. Argentina Zoogeogr., **4:** 137–144, 2 pls.

DERBY, ORVILLE A.

1879. On the plague of rats in Brazil. Nature, **20:** 65.

DICE, LEE R.

1939. Variation in the cactus mouse, *Peromyscus eremicus*. Contr. Lab. Vert. Gen. Univ. Michigan, no. 8: 27 pp.

DIDIER, ROBERT

1959. Note sur les os péniens des rongeurs collectés au Pérou par J. Dorst. Mammalia, **23:** 172–179, 8 figs.

DORST, J.

1958. Contribution a l'étude écologique des rongeurs des hauts plateaux du Pérou Méridional. Mammalia, **22:** 547–565.

ELLERMAN, JOHN R.

1941. The families and genera of living rodents. British Museum (Natural History). i–xii+690 pp., 50 figs.

FERRIS, F. F.

1919–1935. Contributions to a monograph of the sucking lice. Stanford Univ. Publ., Univ. Ser. Biol. Sci., **2**: 634 pp. (appeared in 8 parts).

FERRIS, G. F., and C. J. STOJANOVICH

1951. The sucking lice. Mem. Pacific Coast Ent. Soc., **1**: 320+ix pp., 124 figs.

FITCH, HENRY S., and DENNIS G. RAINEY

1956. Ecological observations of the woodrat, *Neotoma floridana*. Univ. Kansas Mus. Nat. Hist., **8**: 499–533, 3 figs.

GILMORE, RAYMOND M.

1947. Cyclic behavior and economic importance of the rata muca (*Oryzomys*) in Peru. Jour. Mammal., **28**: 231–240.

GIOVANNANI, M., L. G. C. VELLOZO, and G. V. L. KUBIAK

1946. Sobre as "ratadas" do primeiro planalto Paraense. Arq. Biol. Tec., Curitiba, Paraná, **1**: 185–195, pls. 52–60.

GYLDENSTOLPE, NILS

1932. A manual of Neotropical sigmodont rodents. Kungl. Svensk. Vetenskapsakad. Handl., (3), **11**: 164 pp., 18 pls.

HARPER, JOHN L., J. N. CLATWORTHY, I. H. MCNAUGHTON, and G. R. SAGAR

1961. The evolution and ecology of closely related species living in the same area. Evolution, **15**: 209–227.

HARRIS, NORMAN O., ROY B. MEFFERD, JR., and SALVATORE R. RESTIVO

1960. Dental changes induced in rats by chronic exposure to adverse environment. American Jour. Physiol., Washington, **198**: 476–480, 2 figs., 1 table.

HARRISON, G. AINSWORTH

1958. The adaptability of mice to high environmental temperatures. Jour. Experiment. Biol., **35**: 892–901.

HATT, ROBERT T.

1932. The vertebral column of ricochetal rodents. Bull. Amer. Mus. Nat. Hist., **63**: 599–714, 27 figs.

HERSHKOVITZ, PHILIP

1944. A systematic review of the Neotropical water rats of the genus *Nectomys* (Cricetinae). Univ. Michigan Mus. Zool., Misc. Publ. no. 58: 101 pp., 5 figs., 2 maps, 4 pls.

1955. South American marsh rats, genus *Holochilus*, with a summary of sigmodont rodents. Fieldiana: Zool., **37**: 639–687, figs. 139–144, pls. 17–29.

1960. Mammals of northern Colombia, preliminary report no. 8: Arboreal rice rats, a systematic revision of the subgenus *Oecomys*, genus *Oryzomys*. Proc. U. S. Nat. Mus., **110**: 513–568, 6 figs., 12 pls.

HINTON, M. A. C.

1926. Monograph of the voles and lemmings (Microtinae), British Museum (Natural History). 488 pp., 110 figs., 15 pls.

HOFFMEISTER, DONALD F.

1951. A taxonomic and evolutionary study of the piñon mouse, *Peromyscus truei*. Illinois Biol. Monogr. 21, no. 4: 104 pp., 24 figs., 5 pls.

HOOPER, EMMET T.

1952. A systematic review of the harvest mice (genus *Reithrodontomys*) of Latin America. Univ. Michigan Mus. Zool., Misc. Publ. no. 77: 255 pp., 24 figs., 9 pls.

1957. Dental pattern in mice of the genus *Peromyscus*. Univ. Michigan Mus. Zool., Misc. Publ. no. 99: 55 pp., 24 figs., 4 tables.

1959. The glans penis in five genera of cricetid rodents. Univ. Michigan Mus. Zool., Occ. Pap. no. 613: 11 pp., 5 pls.

1960. The glans penis in *Neotoma* (Rodentia) and allied genera. Univ. Michigan Mus. Zool., Occ. Pap. no. 618: 21 pp., 11 pls.

HOPKINS, G. H. E.

1949. The host-associates of the lice of mammals. Proc. Zool. Soc. London, **119**, (2): 387–604.

HOPKINS, G. H. E., and M. ROTHSCHILD

1953–1956. An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History), with keys and short descriptions for the identification of families, genera, species and subspecies of the orders. 1, Tungidae and Pulicidae: xv+361 pp., 465 figs., 45 pls., 1 map, 1953. 2, Coptopsyllidae, Vermypsyllidae, Stephanocircidae, Ischnopsyllidae, Hypsophthalmidae and Xiphiopsyllidae: xi+445 pp., 707 figs., 32 pls., 1 map, 1956.

HUMMELINCK, P. WAGENAAR

1940. Studies on the fauna of Curaçao, Aruba, Bonaire and the Venezuelan Islands. **1**: 1–130, 16 pls. The Hague.

HUSSON, A. M.

1960. Studies on the fauna of Curaçao and other Caribbean Islands, **10**, (43): 33–40, fig. 7, pls. 6–7.

JOHNSON, PHYLLIS T.

1957. A classification of the Siphonaptera of South America, with descriptions of new species. Mem. Ent. Soc. Washington, no. 5: 798 pp., 114 plates in text.

JORDAN, DAVID STARR

1888. A manual of the vertebrate animals of the northern United States. Ed. 5, 375 pp.

KÜHLHORN, FRIEDRICH

1952. Beobachtungen über die Biologie von *Hesperomys musculinus* Thomas. Zeitschr. Säuget., **18**: 116–124.

1954. Säugetierkundliche Studien aus Süd-Mattogrosso. 2. Teil: Edentata; Rodentia. Säugetierk. Mitt., **2**: 66–72.

LANDRY, S. O., JR.

1957. Factors affecting the procumbency of rodent upper incisors. Jour. Mammal., **38**: 223–234, 5 figs.

LAURIE, E. M. O.

1946. The reproduction of the house mouse (*Mus musculus*) living in different environments. Proc. Roy. Soc. London, (B), **133**: 248–281.

MANN, F. G.

1945. Mamíferos de Tarapacá. Biológica, fasc. 2, pp. 23–98, 44 figs., 37 pls.

MARTIN, EDWIN P.

1956. A population study of the prairie vole (*Microtus ochrogaster*) in northeastern Kansas. Univ. Kansas Mus. Nat. Hist., **8**: 361–416, 19 figs.

MERRIAM, C. HART

1894. A new subfamily of murine rodents—the Neotominae—with description of a new genus and species and a synopsis of the known forms. Proc. Philadelphia Acad. Nat. Sci., pp. 225–249, 5 figs.

ODUM, E. P.

1955. An eleven year history of a *Sigmodon* population. Jour. Mammal., **36**: 368–378, 4 figs., 1 pl.

OGLE, CORDELIA

1934a. Adaptation of sexual activity to environmental stimulation. American Jour. Physiol., **107**: 628–634.

1934b. Climatic influence on the growth of the male albino mouse. American Jour. Physiol., **107**: 635–640.

OSGOOD, W. H.

1916. Mammals of the Collins-Day South American Expedition. Field Mus. Nat. Hist., Zool. Ser., **10**: 199–216, pls. 6, 7.

1943. The mammals of Chile. Field Mus. Nat. Hist., Zool. Ser., **30**: 268 pp., 33 figs., 10 maps.

1944. Nine new South American rodents. Field Mus. Nat. Hist., Zool. Ser., **29**: 191–204.

1947. Cricetine rodents allied to *Phyllotis*. Jour. Mammal., **28**: 165–174.

PACKARD, ROBERT L.

1960. Speciation and evolution of the pygmy mice, genus *Baiomys*. Univ. Kansas Publ., Mus. Nat. Hist., **9**: 579–670, 4 pls., 12 figs.

PEARSON, O. P.

1951. Mammals in the highlands of southern Peru. Bull. Mus. Comp. Zool., **106**: 117–174, 8 pls.

1958. A taxonomic revision of the rodent genus *Phyllotis*. Univ. California Publ. Zool., **56**, (4): 391–496, pls. 6–13, 21 figs.

PEREIRA, C.

1941. Sobre as "ratadas" no sul do Brasil e o ciclo vegetativo das Taquaras. Arq. Inst. Biol. São Paulo, **12**: 175–196, 4 pls.

PHILIPPI, F.

1879. A plague of rats. Nature, **20**: 530.

PHILIPPI, R. A.

1900. Figuras i descripciones de los murideos de Chile. An. Mus. Nac. Chile, Zool. Entr., **14a**, 70 pp., 25 pls.

PHILIPPI, R. A., and L. LANDBECK

1858. Beschreibung einiger neuen chilenischen mause. Arch. Naturg., **24**, 1: 77–82.

RABOR, D. S.

1955. Notes on mammals and birds of the central northern Luzon highlands, Philippines. Silliman Jour., **2**: 193–218.

ROONWAL, M. L.

1949. Systematics, ecology and bionomics of mammals studied in connection with tsutsugamushi disease (scrub typhus) in the Assam-Burma War Theatre. Trans. Nat. Inst. Sci. India, **3**: 67–122, 3 figs., 6 pls., 15 tables.

SCHAUB, S.

1925. Die hamsterartigen Nagetiere des Tertiärs und ihre lebenden Verwandten. Abh. Schweiz. Pal. Ges., **45**: 114 pp., 15 figs., 5 pls.

SCHAUB, S., and H. ZAPFE

1953. Die Fauna der miozänen Spaltenfüllung von Neudorf an der March (CSR). Sitzb. Akad. Wiss., Wien, **162:** 181–215, 5 figs., 3 pls.

SCHEFFER, V. B.

1955. Body size with relation to population density in mammals. Jour. Mammal., **36:** 493–515.

SCHNEIDER, CARLOS O.

1946. Catálogo de los mamíferos de la provincia de Concepción. Bol. Soc. Biol. Concepción [Chile], **21:** 67–83.

SEEVERS, C. H.

1955. A revision of the tribe Amblyopinini: staphylinid beetles parasitic on mammals. Fieldiana: Zool., **37:** 211–264, figs. 28–44.

SIMPSON, G. G.

1936. Studies of the earliest mammalian dentitions. Dental Cosmos, Aug., Sept., pp. 1–24 (separate), 10 figs.

SNYDER, D. P.

1956. Survival rates, longevity and population fluctuations in the white-footed mouse, *Peromyscus leucopus*, in southeastern Michigan. Univ. Michigan Mus. Zool., Misc. Publ. no. 95: 33 pp.

STEHLIN, H. G., and S. SCHAUB

1951. Die Trigonodontie der simplicidentaten Nager. Schweiz. Pal. Abh., Basel, **67:** 385 pp., 620 figs.

STIRTON, R. A.

1935. A review of the Tertiary beavers. Bull. Geol. Sci., Univ. California Publ., **23:** 391–458, 142 figs., 1 map, 2 charts.

TATE, G. H. H.

1932a. The South American Cricetidae described by Felix Azara. Amer. Mus. Nov., no. 557: 1–5.

1932b. The taxonomic history of the South American cricetid genera *Euneomys* (subgenera *Euneomys* and *Galenomys*), *Auliscomys*, *Chelemyscus*, *Chinchillula*, *Phyllotis*, *Paralomys*, *Graomys*, *Eligmodontia* and *Hesperomys*. Amer. Mus. Nov., no. 541: 1–21.

THOMAS, OLDFIELD

1884. On a collection of Muridae from central Peru. Proc. Zool. Soc. London, **1884:** 447–458, pls. 42–44.

1888. On a new and interesting annectant genus of the Muridae with remarks on the relation of the Old- and New-World members of the family. Proc. Zool. Soc. London, **1888:** 130–135, pl. 5.

1893. On some mammals from central Peru. Proc. Zool. Soc. London, **1893:** 331–341, pls. 28–29.

1896. On the genera of rodents: an attempt to bring up to date the current arrangement of the Order. Proc. Zool. Soc. London, **1896:** 1012–1028.

1897. On some small mammals from Salta, N. Argentina. Ann. Mag. Nat. Hist., (6), **20:** 214–218.

1898a. On some mammals obtained by the late Mr. Henry Durnford in Chubut, E. Patagonia. Proc. Zool. Soc. London, **1898:** 210–212.

1898b. On the small mammals collected by Dr. Borelli in Bolivia and northern Argentina. Boll. Mus. Zool. Anat. Comp., Torino, **13**, no. 315: 1–4.

1899. Descriptions of new neotropical mammals. Ann. Mag. Nat. Hist., (7), **4:** 278–288.

1900. New Peruvian species of *Conepatus*, *Phyllotis* and *Akodon*. Ann. Mag. Nat. Hist., (7), **6**: 466–469.

1902. On mammals collected by Perry O. Simons in the southern part of the Bolivian plateau. Ann. Mag. Nat. Hist., (7), **9**: 222–230.

1912. New bats and rodents from South America. Ann. Mag. Nat. Hist., (8), **10**: 403–411.

1913. On small mammals collected in Jujuy by Señor E. Budin. Ann. Mag. Nat. Hist., (8), **11**: 136–143.

1916a. On the grouping of the South American Muridae that have been referred to *Phyllotis*, *Euneomys* and *Eligmodontia*. Ann. Mag. Nat. Hist., (8), **17**: 139–143.

1916b. Notes on Argentine, Patagonian and Cape Horn Muridae. Ann. Mag. Nat. Hist., (8), **17**: 182–187.

1918. A new species of *Eligmodontia* from Catamarca. Ann. Mag. Nat. Hist., (9), **2**: 482–484.

1919a. On small mammals from Catamarca. Ann. Mag. Nat. Hist., (9), **3**: 115–118.

1919b. On small mammals collected by Sr. E. Budin in northwestern Patagonia. Ann. Mag. Nat. Hist., (9), **3**: 199–212.

1919c. On small mammals from "Otro Cerro," northeastern Rioja, collected by Sr. E. Budin. Ann. Mag. Nat. Hist., (9), **3**: 489–500.

1919d. List of mammals from the highlands of Jujuy, north Argentina, collected by Sr. E. Budin. Ann. Mag. Nat. Hist., (9), **4**: 128–135.

1926a. The Godman-Thomas expedition to Peru. I. On mammals collected by Mr. R. W. Hendee near Lake Junín. Ann. Mag. Nat. Hist., (9), **17**: 313–318.

1926b. The Spedan-Lewis South American Exploration—III. On mammals collected by Sr. Budin in the province of Tucumán. Ann. Mag. Nat. Hist., (9), **17**: 602–609.

1927. The *Octodon* of the highlands near Santiago. Ann. Mag. Nat. Hist., (9), **19**: 556–557.

TRAUB, R.

1952. Records and descriptions of fleas from Peru. Proc. Ent. Soc. Washington, **54**: 1–22.

URIARTE, L., and N. MORALES V.

1935. A propósito de peste en roedores agrestes de la Argentina. Rev. Inst. Bacteriológico, **7**: 185–212, pls. 2–3, map.

VANZOLINI, P. E., and L. R. GUIMARAES

1955. Lice and the history of South American land mammals. Rev. Brasil. Ent., **3**: 13–46, 4 figs.

VORONTSOV, N. N.

1957. Structure of the stomach and the relative development of parts of the gut in hamsters (Cricetinae, Rodentia, Mammalia) of the Palaearctic and the New World. Doklady, Akademia Nauk, SSSR, **117**, (3): 526–529 (in Russian; English translation in "A translation of Doklady" published by the American Institute of Biological Sciences, Nov.–Dec., 1957).

1959a. The systematics of hamsters (Cricetinae) in the sphere of the world fauna and their phylogenetic relations. Bull. Mosk. Ochestv. Ispyt. Prirody Otdel Biol., **64**, (5): 134–137 (in Russian; English abstract in Biol. Abstr., **36**: 42974, July 1, 1961).

1959b. The geographical distribution of hamsters (Cricetinae) and some problems concerned with the zoogeography of the New World. Bull. Mosk. Ochestv. Ispyt. Prirody Otdel Biol., **64**, (5), 137–139 (in Russian).

1960a. The rate of evolution in Cricetinae and certain agents by which it is determined. Doklady, Akademia Nauk, SSSR, **133**, (4): 980–983, 1 fig. (in Russian; English translation in "A translation of Doklady," published by the American Institute of Biological Sciences, Jan.–Feb., 1961).

1960b. The ways of food specialization and evolution of the alimentary system in Muroidea. International Symposium Theriologicum, Brno, Acad. Scient. Bohemosloveniae, pp. 155–158 (mimeograph in English).

VIEIRA, C.

1953. Roedores e lagomorfos do estado de São Paulo. Arq. Zool. São Paulo, **8**: 129–168.

WAGNER, J. A.

1843. Die Säugthiere in Abbildungen nach der Natur mit Beschreibungen. Supplement, **3**: xiv+614.

WATERHOUSE, C. R.

1839. The zoology of the voyage of *H.M.S. Beagle*, under the command of Captain Fitzroy, R.N., during the years 1832 to 1836. Part 2. Mammalia, i–ix+i–v+97 pp., 35 pls.

WHARTON, GEORGE W.

1948. Four new Peruvian chiggers (Acarina-Trombiculidae). Psyche, **55**: 87–100, 4 figs.

WHITE, THEODORE E.

1959. The endocrine glands and evolution, no. 3: os cementum, hypsodonty, and diet. Contrib. Mus. Paleo. Univ. Michigan, **13**: 211–265.

WINGE, H.

1887. Jordfundne og nulevende Gnavere (Rodentia) fra Lagôa Santa, Minas Geräes, Brasilien. E. Mus. Lundii, **1**, (3), 200 pp., 8 pls.

WOOD, A. E.

1947. Rodents—a study in evolution. Evolution, **1**: 154–162, 5 figs.

1955. A revised classification of the rodents. Jour. Mamm., **36**: 165–187.

WOOD, A. E., and R. W. WILSON

1936. A suggested nomenclature for the cusps of the cheek teeth of rodents. Jour. Pal., **10**: 388–391, 2 figs.

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